Anthropogenic Stressors and Diagnosis of their Effects On Lake Trout Populations in Ontario Lakes

Lake Trout Synthesis
Response to Stress Working Group
1991

Ministry of
Natural
Resources
Ontario

ANTHROPOGENIC STRESSORS AND DIAGNOSIS OF THEIR EFFECTS ON LAKE TROUT POPULATIONS IN ONTARIO LAKES

Lake Trout Synthesis
Response to Stress Working Group
1991

D. O. Evans
Research Section, Fisheries Branch
P.O. Box 5[illegible] Maple, Ontario L6A 1S9

J. Brisbane
Chatham District
P.O. Box 1168, Chatham, Ontario N7M 5L8

J. M. Casselman
Lake Ontario Research Unit
R.R. 4, Picton, Ontario K0K 2T0

K. E. Coleman
Eastern Region
Concession Road, Kemptville, Ontario K0G 1J0

C. A. Lewis
Lake Ontario Research Unit
R.R. #4, Picton, Ontario K0K 2T0

P. G. Sly
Rawson Academy of Aquatic Science
404, 1 Nicholas Street, Ottawa, Ontario K1N 7B7

D. L. Wales
Fisheries Branch, Whitney Block
99 Wellesley Street East, Toronto, Ontario M7A 1W3

C. C. Willox
Lake Simcoe Fisheries Assessment Unit
R.R. 2, Sutton West, Ontario L0E 1R0

Ontario Ministry of Natural Resources

93-01595/

TABLE OF CONTENTS

Abstract iv

Introduction 1
The Concept of Ecological Stress 2
Definition of Stress 3
Stressors Potentially Affecting Lake Trout Communities 5
Life History of Lake Trout in Relation to Major Stressors 7
Spawning 7
Incubation 8
Early Life Stages 8
Juveniles 9
Adults 10

The Geographic Distribution of Lake Trout Populations in Ontario and Associated Stressors 11
Status of the Lake Trout Resource 11
Distribution of Major Stressors 16

Effects of the Major Stressors 20
Exploitation 20
Types of Exploitation 20
Introductions, Invasions and Lake Trout Stocking 27
Exotic Species 28
Indigenous Species 31
Invertebrates 33
Supplemental Lake Trout Stocking 34
Interactions Involving Introductions and Other Stressors 35
Habitat Modifications 37
Description of Physical Habitat 37
Stressors of the Physical Habitat of Lake Trout 40
Watershed Modifications 46
Evaluation of Stressors and Impacts 46
Domestic and Industrial Effluents 50
Domestic Sewage 51
Industrial Sewage 53
Long Range Transport of Pollutants 56
Acidic Deposition 57
Mercury Deposition 59
Lead Deposition 61
Copper Deposition 63
Cadmium Deposition 64

Discussion 65
Lake Trout Response-to-Stress Syndrome 66
Patterns of Population Response to Stress 67
Indicators of Stress 70
First Order Indicators 70
Second Order Indicators 71
Lake Trout Population Status and Response Under Stress 72
Diagnosis of Stress in Lake Trout Populations 80
Unifying Themes 81
Interpretation of Diagnostic Information 82

Management Implications 84
Status of the Lake Trout Resource 84
Major Stressors 85
Exploitation 85
Introductions 86
Habitat Modifications 87
Watershed Modifications 87
Domestic and Industrial Effluents 88
Long-range Transport of Atmospheric Pollutants 89
Diagnosis of Stress 89

Recommendations 91

Acknowledgments 92

References 93

ABSTRACT

Evans, D. O., J. Brisbane, J. M. Casselman, K. E. Coleman, C. A. Lewis, P. G. Sly, D. L. Wales, AND C. C. Willox. 1991. Anthropogenic stressors and diagnosis of their effects on lake trout populations in Ontario lakes. Lake Trout Synthesis, Ont. Min. Nat. Resour., Toronto. 115 p.

We document the status of lake trout (*Salvelinus namaycush*) stocks in Ontario and review the effects and extent of the influences of: exploitation; introduced species and stocks; habitat and watershed manipulations; domestic and industrial effluents; and long-range transport of atmospheric pollutants on lake trout populations. We also propose an approach for field assessment, and diagnosis and attribution of stress effects for these populations. In Ontario, 2318 lakes either presently or once supported lake trout populations. Of these, 1827 lakes contain native populations, but only 1474 of these are self-sustaining wild stocks. The remaining populations are either introduced (222), extinct or lost stocks (122), or stocks of unknown history (83). Based on our survey of Ontario fisheries managers, the major stressors affecting lake trout populations are overexploitation, habitat degradation, and species introductions, the latter including stocking of hatchery-reared lake trout and associated loss of genetic diversity. Lake trout populations respond in predictable ways to anthropogenic influences depending on the intensity and loci of the impairment or mortality, but similar responses can be caused by quite different stressors, simply because they cause mortality at the same life stages. Diagnosis of stress and attribution of causal relationships for lake trout populations, therefore, requires an ecosystem approach that enables an interpretation of population status to be made within an ecosystem context, including knowledge of the status of natural physical environmental variation (including climatic and biotic community states) and specific anthropogenic influences. The lake trout resource has been seriously degraded in southern Ontario (Algonquin, Central, Eastern regions) as only 33% of the stocks in this area are wild, self-sustaining native populations. Similarly, in the Northern and Northeastern regions of Ontario, only 42% and 54% of the native lake trout stocks are self-sustaining. Ecosystem and management objectives and actions are urgently needed to protect the integrity of the remaining wild lake trout resource. Improved approaches to rehabilitation are also needed to restore those populations that have already been damaged.

INTRODUCTION

The objective of this report is to provide a synthesis of existing data and information about the influence of a wide range of human activities (anthropogenic stressors) on lake trout (*Salvelinus namaycush*) populations in Ontario lakes. Emphasis was placed on characterization of the stresses in terms of when and where they occur and how they operate. Our approach is framed by a set of key questions as follows:

- What is the geographic distribution of the lake trout resource and associated anthropogenic stressors;
- What are the most important sources of stress acting on lake trout populations in Ontario lakes;
- How do the stressors operate;
- How do lake trout populations respond to stress; and
- Is it possible to establish causal linkages between stressors and changes in lake trout population structure or production.

These questions are fundamental to the problem of managing lake trout populations in Ontario lakes. These populations are subjected to numerous stressors as a result of human activities on lakes and watersheds, activities which, in some cases, are physically far removed from the lakes actually inhabited by lake trout.

The task of evaluating the effects of stressors on lake trout populations and communities has two major components, that of characterizing the stressors and that of characterizing the structure and dynamics of the lake trout production system, both in the absence and presence of stress. Information is needed about the basic biology of lake trout populations and their dynamics, and about where, when and how the various stressors operate. To address our five original questions, we have organized the report into the following sections:

- review of the basic concept of ecological stress, identification of potential stressors and the vulnerability of the various life history stages of lake trout;
- status of the lake trout resource in Ontario and the distribution of associated stressors;
- review of six major categories of stressors; eutrophication, species introductions, habitat modifications, watershed modifications, domestic and industrial effluents, and long-range transport of atmospheric pollutants;

- discussion of the lake trout response-to-stress syndrome and proposal of indicators for diagnosis of stress response in lake trout populations; and
- discussion of the management implications of our findings.

THE CONCEPT OF ECOLOGICAL STRESS

The concept of ecological stress is widely used among ecologists and resource managers to indicate a broad spectrum of factors, phenomena or agents, usually of anthropogenic origin, that influence the state of ecological systems (Barrett and Rosenberg 1981). Ecological stress tends to be used as a catch-all concept, however, with spatial and temporal dimensions of particular problems often being poorly defined. Only in the most extreme cases has it been possible to establish cause and effect relationships between population or community response and a stressor under field conditions. A fundamental problem in the evaluation of the influence of potential stressors is in deciding when particular factors cease to be a minor stimulus and become stressors. Odum et al. (1979) referred to the subsidy-stress gradient in which man-induced perturbations at one level can enhance response, but cause a degradative response at higher levels. Nutrient addition is one example of this type.

Numerous authors have discussed the concept of stress at the ecosystem and other organizational levels (Barrett and Rosenberg 1981; Pickering 1981; Cairns et al. 1984), often with quite different perspectives. Fish physiologists (e.g. Donaldson 1981; Schreck 1981; Wedemeyer and McLeay 1981) have tended to adopt the concept of Selye (1973) in which the stress is equated with stimulus and the response to stress is seen simply as part of the normal process of maintaining homeostasis in a variable environment. Once certain thresholds of tolerance are exceeded, the organism enters a zone of resistance, and unless the stress is reduced, death occurs. Ecologists borrow from the same concept, but tend to equate stress with perturbations of anthropogenic origin that fall outside the realm of normal spatial and temporal environmental variation. An important distinction is that populations, communities, and ecosystems can have multiple equilibria so that they are not homeostatic in the same sense as organisms.

Populations and communities display quasi-homeostatic responses involving density-dependent feedback mechanisms that provide for compensatory adjustment of birth and death rates. These types of mechanisms include the effect of stock density on recruitment success of populations (Johnson

1976) and compensatory growth and associated changes in maturity and fecundity of fish stocks (Healey 1978a). Similarly, when the cost of searching for and feeding on a primary prey species becomes energetically unprofitable at low density, predators will switch to alternative sources of food. This represents one mechanism of self-organization which influences community stability by regulating prey abundances (Evans et al. 1987). The same regulatory mechanisms would be expected to operate at the population and community levels, whether a stress factor is of natural or anthropogenic origin. Indeed, populations exist in only one of three states: they can increase, decrease or stay at the same level. These states are achieved through processes that modify birth and death rates, thereby modifying the net reproductive rate of a population (Jensen 1985).

Populations, communities and ecosystems have the flexibility of being able to exist in different equilibrium states, wherein patterns of energy flow can be dramatically different (Peterman et al. 1979). Organisms also have some capacity to exist in different states, but generally are more constrained by physiological limits and energy requirements for completion of life cycles. Thus, there are fundamental differences between the regulatory mechanisms of organisms and ecosystems, which preclude direct translation of stress concepts and response syndromes from one level of organization to another.

The main distinction, therefore, between the responses of organisms and higher level systems to stress is the nature of the homeostatic response; physiological homeostasis in the case of organisms versus shifting population or community equilibria. The general adaptation syndrome (Selye 1973, 1976) is otherwise similar, involving some initial disruption of the system, followed by resistance and reestablishment of stability or finally, if the stress surpasses some critical threshold, exhaustion culminating with death of the organism or extinction of the population.

Definition of Stress

The phenomenon of ecosystem stress encompasses two components, the stress agent or factor (stressor) and the stress response of the affected system. We recommend an interpretation in which a perturbing factor is identified as the stressor and the response of the system under consideration is the stress response. We suggest that the term stress be reserved for situations in which harmful transformation of a system is induced either directly or indirectly by human activities. We define stress as:

> *a situation in which an anthropogenic stressor acts on a population, community or ecosystem with sufficient effect to cause a prolonged disruption of energy flow and pattern of energy storage, so as to alter the state and stability characteristics of the affected system with a net loss of sustained benefits.*

Within the usual context of natural resource management, ecological stress of this type would be of concern because of the potential for net loss of sustained economic, social, aesthetic, or ecological benefits.

We argue that the stress concept will be most useful in communicating fisheries information and in managing fisheries resources, if it is used in a consistent fashion, hence, the need for an operational terminology. The concept of stress is broad in scope and terminology is far from standardized (Auerbach 1981). Some important advances have been made, however, towards synthesis of existing knowledge of stress responses of living systems (Rapport et al. 1981). These authors draw upon the fundamental arguments and constructs of the general adaptation syndrome of Selye (1973), to develop analogies between human medicine and ecological systems. They also propose qualitative and quantitative approaches for application of stress theory to the diagnosis, prognosis, and treatment of stressed ecosystems. We shall return to their ideas in the final section of this report.

Stress is generally viewed by fisheries biologists as a perturbing force that imposes strain on a living system (Loftus and Regier 1972). Alternatively, stress is often seen by ecologists as a system response to an external stimulus, a stimulus of sufficient magnitude to involve mobilization and redirection of energy resources (Lugo and McCormick 1981). In the latter usage, the stress is the state of the biological system, while the stressor is the situation, condition, agent or intensity of environmental factor that brings about the system response. These usages are not incompatible, indeed the same phenomena are simply being described in slightly different ways.

Factors that cause a change in energy flow in a system can be either beneficial or harmful, depending on their intensity (Odum et al. 1979). Also, in some cases, a decision about the beneficial versus harmful effect of a stressor is, of necessity, based on a subjective evaluation of the system response. For example, an unexploited fish stock would be considered to be unstressed, but would also provide less yield than one subjected to a moderate fishing stress. Selye (1973) recognized an

analogous phenomenon in human physiology, whereby he referred to eustress and distress. Eustress is the case in which some factor stimulates or challenges the system to evoke an adaptive response that is beneficial. The term beneficial can have many meanings, but we use it here in an anthropomorphic sense of self-sustaining benefit. Distress refers to system transformation leading to ultimate system breakdown.

Factors such as fishing or moderate nutrient inputs need not always be considered as stressors and, in some cases, might be usefully employed as management techniques (McFadden 1977; Hyatt and Stockner 1985, respectively, but also see Riebesell 1974 and Rosenzweig 1971). Adoption of the subsidy-stress concept of Odum et al. (1979) adequately deals with the duality of beneficial versus harmful effects. One remaining difficulty is to decide on the threshold between enhancement and degradative effects. For lake trout populations, loss or gain of self-sustained productivity can serve as a relatively precise criterion.

STRESSORS POTENTIALLY AFFECTING LAKE TROUT COMMUNITIES

Within each of six major generic stress areas (exploitation, species introductions, habitat modifications, watershed modifications, domestic and industrial effluents, and long-range transport of atmospheric pollutants), 39 potential stressors have been identified. The complete listing of generic and specific potential stressors that we have considered is presented below:

Exploitation

- Angling (open water)
- Angling (ice)
- Commercial fishing
- Subsistence fishing

Species introductions

- Exotic species
- Indigenous species
- Stocking of hatchery-reared lake trout
- Introduction or invasion of aquatic invertebrates

Aquatic habitat modifications

- Shoreline modifications:construction of jetties, causeways, roads and foundations
- Removal of aggregate from lakes

Navigational dredging
Nearshore and offshore disposal of material
Construction of dams and dykes
Hydrological structures which alter mean lake level, seasonal lake level or water flow regimes
Log booms for sawmill or pulp and paper operations
Wood fibre deposition in lakes
Submerged electrical transmission cables
Other modifications to aquatic habitat

Watershed modifications

Siltation from road construction and maintenance
Culverts and barriers for road construction
Erosion and siltation from forestry practices
Insecticides and herbicides from forestry practices
Nutrient loading from forestry practices
Erosion and siltation from agriculture
Nutrients from agriculture
Insecticides and herbicides from agriculture practices
Construction and development in the watershed
Siltation, minerals and nutrients from fire
Salt and oil dressings on roads
Upstream dams or diversions affecting lake flow regimes
Other watershed modifications

Domestic and industrial effluents

Nutrients from municipal sewage
Contaminants from municipal sewage
Nutrients from cottage and campground effluents
Mining effluents
Pulp and paper effluents
Chemical industry effluents
Thermal effluents
Other municipal and industrial effluents

Long-range transport of atmospheric contaminants

Acidification
Metals
Organics

Two approaches have been taken to assess the possible effects of these potential stressors. First, Ontario fisheries managers were surveyed to determine the perceived importance of these potential stressors, and to identify specific cases where evidence of effects is well documented. The results of this survey are summarized herein and reported in detail in a companion report (Lewis et al. 1990).

Our second approach has been to review the published and unpublished literature concerning the effects of the main generic stressors and their major components.

LIFE HISTORY OF LAKE TROUT IN RELATION TO MAJOR STRESSORS

Spawning

Lake trout in inland lakes in Ontario spawn during the fall (late September to mid-November), in shallow water (1-4 m), along shorelines or shoals that are exposed to the prevailing wind (Martin and Olver 1980). Some riverine stocks in the Great Lakes (Lake Superior) spawn during early September in response to early cooling of flowing water. In general, deeper spawning occurs in the Great Lakes because of their size and hydrodynamics. For instance, in Lake Superior, spawning activity was suggested by Eschmeyer (1954) to occur at depths of greater than 91 m. The spawning substrate is usually broken rubble or angular rock, 3-15 cm in diameter, commonly interspersed with large boulders (Martin and Olver 1980). The substrate is notably free of sand, mud, detritus, and vegetation. Wind and wave action is the primary mechanism keeping the spawning areas clean (Martin and Olver 1980). Substrates of silt, clay, or marl are generally unsuitable for successful reproduction (Marcus et al. 1984). Most spawning takes place from dusk to 23:00 h with males usually preceding the females onto the spawning beds (Martin and Olver 1980). High densities of trout are often found at spawning areas. For example, on one major spawning shoal in Lake Simcoe, 1341 trout were netted over a period of 28 days (McCrimmon 1958). Feeding activity slows during the pre-spawning period (Fry 1939; Martin 1970) and there appears to be no active feeding during the spawning period (Martin and Olver 1980).

The lake trout during spawning and its spawning habitat at all seasons are potentially vulnerable to stressors. As trout congregate on spawning shoals, they are vulnerable to exploitation by angling and especially by nets. Throughout most of Ontario, legislation prohibits sport and commercial fishing during the spawning period; however, in some areas, legal subsistence fishing in treaty areas, or illegal sport or commercial fishing occurs. Unfortunately, the extent and influence of these activities is not well documented.

The availability of lake trout spawning habitat is generally limited in most inland lakes. The limited occurrence of these sites renders the spawning habitat a potentially vulnerable link in the

reproductive cycle. The general vulnerability of nearshore habitats to shoreline modifications and water level changes, therefore is of particular concern. For example, a recent survey of 202 lake trout spawning sites on inland Ontario lakes indicated that 64% had characteristics such as proximity to shorelines and inlets which made them susceptible to influxes of acidic melt water (McMurtry 1986).

Incubation

Many eggs deposited during spawning settle into the interstitial spaces of the substrate. If the rocky substrate is deep enough and the interstices of appropriate dimensions, egg predation is usually not a serious problem (Martin and Olver 1980). Some egg predation undoubtedly occurs, however, in all populations. In their review of the literature, Martin and Olver (1980) listed numerous predators on lake trout eggs including: suckers (Catostomidae), brown bullhead (*Ictalurus nebulosus*), lake whitefish (*Coregonus clupeaformis*), round whitefish (*Prosopium cylindracum*), lake trout, yellow perch (*Perca flavescens*), slimy sculpin (*Cottus cognatus*), fallfish (*Semotilus corporalis*), and crayfish (*Orconectes rusticus*). The principal predators in inland lakes appear to be brown bullhead and white sucker (*Catostomus commersoni*). In lakes Superior and Michigan, however, the principal predators were round whitefish and burbot (*Lota lota*) (Stauffer and Wagner 1979). Introduced species may also have a negative effect if they feed on lake trout eggs or fry.

The incubation period varies between lakes and years. For example, Martin (1956) found that hatching varied from February 15 to March 30 in some Algonquin Park lakes. Incubation varies from 2 to 6 mo in the Great Lakes region, being most brief in Lake Superior river spawning populations and most protracted in Green Lake, Wisconsin (Martin and Olver 1980).

In addition to direct shoreline modifications, spills involving lethal chemicals (domestic/industrial effluents), siltation from road construction (watershed modification) or from nearby dredging or filling (habitat modification) and degradation of organic material (algae, macrophytes, Sly 1988) all have the potential to reduce egg survival.

Early Life Stages

Oxygen depletion of interstitial water within the substrate, due to decomposition of organic material, is a primary concern where excessive nutrient inputs occur. Dissolved oxygen concentrations less than 4.5 mg L^{-1} have been found to retard development, delay hatching, and to cause malformation of embryos (Garside 1959).

DeRoche (1969) found that alevins and fry remained in the rocky littoral zone until water temperature increased to 10°C, at which time they moved directly to deep water (25-35 m). Martin and Olver (1980) noted Eschmeyer's belief that the young moved to deeper water about 1 mo after hatching or at the time of absorption of the yolk sac. Paterson (1968) suggested that with the lack of ice cover, the young moved to deeper water to avoid the light. Recent studies in lakes Superior and Michigan, however, have found young-of-year (YOY) lake trout in relatively shallow water (2-8 m depth) from May to the end of July (Stauffer 1981; Wagner 1981; Peck 1982). In Presque Isle Harbour, Lake Superior, young lake trout were captured using bottom trawls at 2-8 m over rocky and sandy substrates; movement to sandy areas increased from spring through summer. Fry departed the harbour about 12 wk after hatching or 1-2 mo after emergence when water temperatures exceeded 15°C. Once in deeper water, it would seem that young lake trout are relatively free from most stressors, with the important exception of reduced dissolved oxygen, which occurs naturally during summer stratification, and which can be further depressed by high nutrient loads and associated biochemical oxygen demand in the hypolimnion. While in the littoral zone, however, the alevins and fry are vulnerable to many potential stressors, including, for example, inorganic and organic sediments, acidic runoff and associated metals, toxic chemicals in effluents or spills, and predation by introduced species.

Juveniles

Martin (1952) indicated that young trout were found in deeper water than adults during the summer, suggesting the importance of a deep-water sanctuary for survival of young trout and, hence for recruitment. In the deep hypolimnion, young trout are constrained by a new set of factors, including increased competition from cohorts, predation by large piscivores including older lake trout, and limiting conditions of cold temperature and reduced oxygen concentration. Oxygen depletion in the hypolimnion during summer, would be expected to force young trout into shallower depths, where they would be more vulnerable to predation and/or cannibalism.

The dissolved oxygen level of no excess activity (level at which swimming activity is not possible) for yearling lake trout is about 40 mm Hg (2.8 mg L^{-1}) at 10°C and about 60 mm Hg (3.5 mg L^{-1}) at 22°C, and slightly lower at both temperatures for 2 yr-old lake trout (Gibson and Fry 1954). As the level of no excess activity is equivalent to the incipient lethal oxygen tension (Davis 1975), young lake trout would be expected to avoid oxygen levels at or below these values. High rates of cannibalism

on yearling hatchery trout after stocking (Martin and Olver 1980; MacLean et al. 1981) suggests the importance of segregation of adults and juveniles. Hatchery juveniles tend to remain at shallow depths while they become orientated to the lake environment (Casselman 1986). Juveniles begin to become vulnerable to exploitation by anglers at ages 3 to 4 yr, suggesting a change in either distribution or diet, or both. The significance of high quality juvenile habitat for natural recruitment of lake trout is evaluated in detail by Evans et al. (1991).

Adults

The age, length and weight at which lake trout attain first maturity varies between lakes and stocks. Martin and Olver (1980) noted ages range from 4 to 13, while lengths and weights range from 28 to 65 cm and from 0.5 to 2.5 kg, respectively. Males normally mature approximately 1 yr before females (Martin and Olver 1980).

Adult lake trout seem to be somewhat solitary and nomadic. Most movement appears to be in response to factors such as spawning, feeding and changes in environmental conditions, while others may be completely random (Martin and Olver 1980). During the summer period of thermal stratification, lake trout tend to concentrate in deeper, colder waters below the thermocline. During the fall and spring, the species is frequently found in shallow littoral areas of lakes. During the winter, lake trout disperse throughout a wide range of depths. Martin and Olver (1980) noted most trout in smaller inland lakes are caught in less than 10 m of water during the winter. In Lake Simcoe, they are commonly caught at depths of 14-23 m, although they are known to occur at all depths (MacCrimmon and Skobe 1970). In Swan Lake, Alberta, Paterson (1968) suggested that lake trout inhabited all depths during the winter.

Adult lake trout will take most available aquatic prey, including annelids, crustaceans, insects, molluscs and fishes, although they are primarily piscivorous (Martin and Olver 1980). Growth rates between stocks are extremely variable and directly related to the quantitative and qualitative nature of the food supply (Martin and Olver 1980).

Of all the stressors associated with humans, adult lake trout are probably most vulnerable to exploitation. They are readily taken by sport and commercial fishermen throughout the open seasons. As well, they are vulnerable to illegal exploitation when concentrated during the fall spawning period.

Stressors, such as domestic and industrial effluents, watershed and habitat modifications, and acidification could also have a direct impact on the adult life stage, through numerous direct and indirect pathways.

THE GEOGRAPHIC DISTRIBUTION OF LAKE TROUT POPULATIONS IN ONTARIO AND ASSOCIATED STRESSORS

In December 1987, a questionnaire (Lewis et al. 1990) was sent to all Ontario Ministry of Natural Resources (OMNR) districts with lake trout lakes. The purpose of this questionnaire was 3-fold: to update an earlier lake trout atlas (Olver 1980) to provide new information about population status of all lakes; to determine the perception of managers about the distribution and effects of various stressors in their districts; and to determine the availability of lake-specific information (beyond that collected through standard lake surveys) on population attributes, water level fluctuations, access, development, water chemistry (oxygen-temperature profiles), spawning shoals, introductions and a variety of other stressors.

Questionnaires were sent to the 39 OMNR districts with lake trout lakes, and to the Leslie M. Frost Natural Resources Centre. Most questionnaires were completed by district biologists and fisheries management officers.

STATUS OF THE LAKE TROUT RESOURCE

The results of the lake trout questionnaire (Lewis et al. 1990) provide information concerning the location and population status of 2318 lakes (exclusive of the Great Lakes) which presently support, or once supported, lake trout. All lakes were assigned a status code identifying the type of lake trout stock that is supported at this time (Table 1). Most of the lakes (91%) are located in the Northeastern, Northwestern, Algonquin and North Central regions of Ontario (35%, 22%, 19%, and 15%, respectively) (Table 2; Fig. 1[1]). The total number of lakes having extant lake trout populations is 2196 which adds 72 lakes to the listing in the 1980 lake trout atlas (Olver 1980).

The status of these populations is summarized by administrative region and district in Tables 2 and 3. A large proportion of the populations (1827 lakes, 79%) are of native origin (categories N1 to

[1]Figures in end pocket.

N6). Most of the lakes in the Northwestern (99%) and North Central (89%) regions are in category N1 - native populations, never stocked, and self-sustaining (Table 2; Fig. 2). The percentage of lakes in the N1 category decreases in a southward direction, with only 10% of the lakes in Eastern Region and none of those in Central or Southwestern regions in this category. This reflects, in part, lesser human influence in the north compared to the south.

Only six lakes were classified as N2 (native population, natural reproduction, partly self-sustaining, supplemented by plantings of native stock). In contrast, 269 lakes, or 12% of the lakes in all categories were category N3 (similar to N2 but supplemented by plantings of non-native stock). This reflects the widespread practice in Ontario of stocking with non-native stocks. Categories N4 and N5 represent those lakes with little or no natural reproduction, and where the populations are maintained by plantings (native and non-native stock, respectively). There are 60 of these in total. Finally, there are 18 lakes (category N6) with a native remnant population, which is self-sustaining, but supplemented by plantings of splake (*Salvelinus namaycush* x *S. fontinalis*). These are almost exclusively in the Northeastern, Algonquin, and Eastern regions.

TABLE 1. Classification scheme for the status of lake trout populations in Ontario lakes. Native lake trout refers to the native parental stock of a particular lake, and non-native refers to a parental stock from another lake.

Stock status	Criteria
N1	Native population: natural reproduction, self-sustaining, unstocked
N2	Native population: natural reproduction, partly self-sustaining, supplemented by plantings of native stock
N3	Native population: natural reproduction, partly self-sustaining, supplemented by plantings of non-native stock
N4	Native population: little or no reproduction, population maintained by plantings of native stock
N5	Native population: little or no reproduction, population maintained by plantings of non-native stock
N6	Native remnant population: self-sustaining, supplemented by plantings of F_1 splake
I1	Introduced population: no native stock, self-sustaining
I2	Introduced population: no native stock, population maintained by plantings
U	History unknown
E	Extinct population: native or introduced population which disappeared from a lake after a known period of natural reproduction
L	Lost population: population of unknown history and reproductive status which disappeared from a lake
O	Other: specify

TABLE 2. Population status (see Table 1) for lake trout lakes by region as reported in Lewis et al. (1990). Regions of Ontario are as follows: NWR - Northwestern Region; NCR - North Central Region; NR - Northern Region; NER - Northeastern Region; AR - Algonquin Region; ER - Eastern Region; CR - Central Region; SWR - Southwestern Region.

Region	N1	N2	N3	N4	N5	N6	Tot-N	I1	I2	I	Tot-I	U	E	L	O	Total	% of prov. total
NWR no.	512	0	2	0	0	1	515	0	1	0	1	0	1	0	2	519	22
%	99																
NCR no.	301	0	16	0	0	0	317	4	4	3	11	2	1	0	7	338	15
%	89																
NR no.	51	0	9	0	1	0	61	5	44	2	51	5	1	0	3	121	5
%	42																
NER no.	436	6	108	1	13	5	569	48	48	1	97	54	54	23	9	806	35
%	54																
AR no.	166	0	99	3	29	6	303	6	45	1	52	22	20	13	41	451	19
%	37																
ER no.	8	0	35	0	12	6	61	3	3	0	6	0	6	3	2	78	3
%	10																
CR no.	0	0	0	1	0	0	1	0	3	0	3	0	0	0	0	4	.2
%																	
SWR no.	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	
Total	1474	6	269	5	55	18	1827	66	149	7	222	83	83	39	64	2318	100
%	64		12		2	1	79	3	6		10	4	4	2	3	100	

TABLE 3. Population status for lake trout lakes in Ontario by OMNR districts and regions. Region codes are as in Table 2 and District codes refer to OMNR districts reported in Lewis et al. (1990).

District	N1	N2	N3	N4	N5	N6	Tot-N	I1	I2	I	Tot-I	U	E	L	O	Total
11	116	0	0	0	0	0	116	0	0	0	0	0	0	0	0	116
12	100	0	0	0	0	0	100	0	0	0	0	0	0	0	0	100
13	55	0	0	0	0	0	55	0	0	0	0	0	0	0	0	55
14	115	0	1	0	0	1	117	0	0	0	0	0	0	0	2	119
15	102	0	0	0	0	0	102	0	0	0	0	0	0	0	0	102
16	24	0	1	0	0	0	25	0	1	0	1	0	1	0	0	27
NWR no.	512	0	2	0	0	1	515	0	1	0	1	0	1	0	2	519
21	153	0	0	0	0	0	153	0	0	0	0	0	0	0	0	153
22	17	0	0	0	0	0	17	1	0	1	2	0	0	0	0	19
23	35	0	0	0	0	0	35	2	3	0	5	1	0	0	0	41
24	33	9	9	9	9	9	33	1	1	1	3	1	1	9	9	38
25	63	0	16	0	0	0	79	0	0	1	1	0	0	0	7	87
NCR no.	301	0	16	0	0	0	317	4	4	3	11	2	1	0	7	338
31	22	0	4	0	0	0	26	1	0	1	2	2	1	0	0	31
32	0	0	0	0	0	0	0	0	10	0	10	0	0	0	0	10
33	15	0	0	0	1	0	16	0	13	0	13	3	0	0	2	34
34	0	0	0	0	0	0	0	0	4	1	5	0	0	0	0	5
35	0	0	0	0	0	0	0	1	5	0	6	0	0	0	0	6
36	6	0	5	0	0	0	11	1	9	0	10	0	0	0	1	22
37	4	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4
38	4	0	0	0	0	0	4	2	3	0	5	0	0	0	0	9
NR no.	51	0	9	0	1	0	61	5	44	2	51	5	1	0	3	121
41	159	0	12	0	4	1	176	21	14	0	35	20	0	1	0	232
42	49	2	40	0	0	2	93	0	0	0	0	0	0	0	5	98
43	2	0	19	1	1	1	24	1	14	0	15	3	0	1	1	44
44	77	0	13	0	6	1	97	4	2	0	6	1	3	0	0	107
45	41	4	8	0	2	0	55	9	13	0	22	18	43	14	0	152
46	64	0	13	0	0	0	77	0	5	0	5	10	7	3	2	104
47	44	0	3	0	0	0	47	13	0	1	14	2	1	4	1	69
NER no.	436	6	108	1	13	5	569	48	48	1	97	54	54	23	9	806

TABLE 3. Continued.

District	N1	N2	N3	N4	N5	N6	Tot-N	I1	I2	I	Tot-I	U	E	L	O	Total
51	128	0	3	3	0	2	136	3	0	0	3	3	0	0	2	144
52	3	0	28	0	6	0	37	0	7	0	7	1	8	1	6	68
53	13	0	18	0	6	0	37	2	12	0	14	0	0	1	22	74
54	14	0	23	0	5	3	45	0	18	1	19	9	3	0	8	84
55	6	0	6	0	8	1	21	0	5	0	5	6	9	0	3	44
56	1	0	14	0	2	0	17	1	3	0	4	3	0	11	0	35
57	1	0	7	0	2	0	10	10	0	0	0	0	0	0	0	10
AR no.	166	0	99	3	29	6	303	6	45	1	52	22	20	13	41	451
61	0	0	2	0	2	1	5	0	0	0	0	0	2	0	0	7
63	0	0	0	0	0	0	0	2	1	0	3	0	0	0	0	3
64	0	0	9	0	8	0	17	0	2	0	2	0	1	0	0	20
66	8	0	24	0	2	5	39	1	0	0	1	0	3	3	2	48
ER no.	8	0	35	0	12	6	61	3	3	0	6	0	6	3	2	78
71	0	0	0	0	0	0	0	0	3	0	3	0	0	0	0	3
74	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1
CR no.	0	0	0	1	0	0	1	0	3	0	3	0	0	0	0	4
83	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1
SWR no.	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1
Total	1474	6	269	5	55	18	1827	66	149	7	222	83	83	39	64	2318
%	64		12		2	1	79	3	6		10	4	4	2	3	100

A total of 222 lakes, or 10% of the total, are listed as having lake trout populations which were introduced (Table 2; Fig. 3). Most of these are in the Northern, Northeastern, and Algonquin regions. Two-thirds of these are considered to be maintained by plantings; the other one-third - mostly in the Northeastern Region - are now considered self-sustaining. Eighty-three lakes (4%) were classified as "history unknown"; most of these are in the Northeastern and Algonquin regions (Table 2; Fig. 4).

A total of 83 lakes (4%) are listed where lake trout are now considered extinct, including 54 in Northeastern Region and 20 in Algonquin Region (Table 2; Fig. 4). A further 39 lakes are considered to have lost their lake trout stocks. In these cases, the previous status and reproductive history are unknown. Some of these lakes may never have supported naturally-reproducing populations of lake trout. Finally, 64 lakes were classified as "other" status (Table 2; Fig. 4). Populations classified as other include the following: (1) population status not verified during the most recent survey; (2) a remnant population exists but not stocked with F_1 splake; (3) the population has not been evaluated following a change in the stocking regime; and (4) an introduced population, some natural reproduction, and supplemented by stocking.

DISTRIBUTION OF MAJOR STRESSORS

Exploitation by angling, effluents from cottages and campgrounds, construction and development in the watershed, and stocking of non-native lake trout are the stressors perceived by managers as having the most impact on lake trout populations (Lewis et al. 1990). This perception was reiterated in Part C of the lake trout questionnaire in which respondents were asked to list the top three management concerns with respect to lake trout in their districts. Exploitation, habitat degradation/loss, and species introductions were viewed to be the three most important management concerns (Table 4). Many of the other concerns identified relate to the first two. For example, access and meeting angler needs both relate to exploitation stress and regulation of fishing, while acidification and development relate to habitat degradation and loss.

Many of the most important stressors can be linked to the degree of development on the lake and its watershed. Development influences access, harvest, and land use. The lake trout questionnaire (Lewis et al. 1990) asked what percent of lake trout lakes in each district were in the following development categories: high, medium, low and none. The results (Table 5) reveal increasing development from north to south. Similarly, access to the lake trout resource is greatest in the southern regions of the province (Table 6).

Although managers perceived many of the stressors to be acting on lake trout populations in their districts, there were many cases where the impacts were unknown. Documentation of effects is rare.

The questionnaire provided an understanding of manager's perceptions of stressors acting on lake trout resources. However, evaluation of the accuracy of those perceptions is difficult. In the area of acidic precipitation, there are independent data about the distribution of this stressor and a quantified estimate of impacts on lake trout. These data provide a check against the perceptions of the field managers. Field managers perceived this stress to be present over a much broader area of the province than provincial estimates indicate. It is possible that managers interpreted the questionnaire to be asking what percent of lake trout lakes in your district are exposed to acidic deposition, in which case, the result is reasonable. On the other hand, many respondents indicated that they did not know the percent of their lake trout lakes that are exposed to this stressor, despite the availability of reports that indicate levels of deposition and potential impacts.

Districts were asked to identify the types and amount of information available for individual lake trout lakes (Part C of questionnaire, Lewis et al. 1990). Categories of information requested included population structure data, type of access, presence of dams and degree and timing of water level drawdowns, amount of shoreline development, oxygen and temperature data, spawning shoal assessment, and species introductions. Districts were also asked to rank a number of stressors in terms of

TABLE 4. Management concerns identified by districts, as reported in the Ontario lake trout questionnaire (Lewis et al. 1990).

Management concern	OMNR districts identifying this concern	No. of districts
Overexploitation	11 12 13 14 15 16 21 22 25 31 36 37 38 41 43 44 45 46 47 51 52 54 55 56 57 61 63 64 66 74	30
Habitat degradation/loss	11 12 13 14 15 16 22 31 36 38 42 44 45 46 54 56 57 61 63 64 66 74	23
Species introductions	11 12 15 25 36 41 42 44 47 54 55 66	12
Access	13 24 25 27 33 34 42 47	8
Development	16 21 24 38 43 56	6
Lack of data on lakes	23 24 33 37 53 57	6
Acidification	33 41 43 46 51 55	6
Loss of genetic integrity	14 45 51 63	4
Meeting needs of anglers	32 35 71 83	4
Rehabilitation/protection of lake trout populations	23 34 52	3
User education	31 37	2
Native subsistence fishing	22	1
Lack of natural reproduction	35	1

TABLE 5. Percent of lake trout lakes in each OMNR district in each development category. Information from Lewis et al. (1990).

	No. of lake trout lakes		Development (% of lake trout lakes)			
District	Total	Excl. E/L[1]	High	Medium	Low	None
11	116	116	5	10	5	80
12	100	100	2	17	27	54
13	55	55	0	<25	25-50	25-50
14	119	119	5	20	10	65
15	102	102	2	12	44	42
16	27	26	23	19	27	30
21	153	153	5	2	9	84
22	19	19	11	5	47	37
23	41	41	3	8	8	81
24	38	37	0	20	10	70
25	87	87	20	20	20	40
31	31	30	4	26	30	40
32	10	10	20	0	0	80
33	34	34	0	7	7	86
34	5	5	0	0	25	75
35	6	6	0	0	0	100
36	22	22	14	36	0	50
37	4	4	0	0	75	25
38	9	9	0	0	0	100
41	232	231	10	15	40	35
42	98	98	5	5	5	85
43	44	43	4	56	4	36
44	107	104	20	70	5	5
45	154	95	5	20	25	50
46	104	94	12	7	6	75
47	69	64	9	18	26	47
51	144	144	5	10	0	85
52	60	51	57	20	23	0
53	74	73	25	53	22	0
54	84	81	75	15	10	0
55	44	35	20	75	5	0
56	35	24	75	25	0	0
57	10	10	0	90	0	10
61	7	5	100	0	0	0
63	3	3	50	50	0	0
64	20	19	15	65	20	0
66	48	42	25	50	0	25
71	3	3	33	0	0	67
74	1	1	100	0	0	0
83	1	1	0	100	0	0

[1]E/L = lakes with lake trout populations extinct or lost.

TABLE 6. Percent of lake trout lakes in each OMNR district for each access category. Information from Lewis et al. (1990).

District	No. of lake trout lakes		Access (% of lake trout lakes)			
	Total	Excl. E/L[1]	High	Medium	Low	None
11	116	116	33	62	0	5
12	100	100	7	92	0	1
13	55	55	<25	(50-75 med-low)		<25
14	119	119	30	50	5	15
15	102	102	10	20	40	30
16	27	26	23	12	27	38
21	153	153	0	58	42	0
22	19	19	37	26	5	32
23	41	41	27	49	4	20
24	38	37	30	60	10	0
25	87	87	50	20	15	15
31	31	30	30	60	0	10
32	10	10	70	20	0	10
33	34	34	68	3	3	26
34	5	5	25	0	75	0
35	6	6	83	0	17	0
36	22	22	68	32	0	0
37	4	4	0	0	0	100
38	9	9	89	0	11	0
41	232	231	35	40	15	10
42	98	98	25	50	5	20
43	44	43	88	9	3	0
44	107	104	80	15	5	0
45	154	95	35	50	5	10
46	104	94	30	23	31	16
47	69	64	20	46	13	21
51	144	144	15	3	82	0
52	60	51	79	21	0	0
53	74	74	85	15	0	0
54	84	81	90	5	5	0
55	44	35	80	10	10	0
56	35	24	75	25	0	0
57	10	10	70	10	20	0
61	7	5	100	0	0	0
63	3	3	50	50	0	0
64	20	19	82	0	18	0
66	48	42	90	0	10	0
71	3	3	33	33	0	34
74	1	1	100	0	0	0
83	1	1	100	0	0	0

[1]E/L = lakes with lake trout populations extinct or lost.

their historical and recent importance for each lake. In total, responses were received for 476 lakes from 39 districts providing an important compilation for sources of data pertaining to lake trout lakes. A summary of the lake-specific data identified in this part of the questionnaire is given in Lewis et al. (1990). Although most lakes had only 1 or 2 yr of data for any given parameter, several lakes were identified that had up to 7 yr of data.

EFFECTS OF THE MAJOR STRESSORS

EXPLOITATION

Fishing acts as a stress on fish populations by causing mortality. Regier and Loftus (1972) and Spangler et al. (1977) provided general overviews about the responses of salmonids and percids to exploitation. Intensive exploitation can have predictable effects on lake trout populations including: declines in abundance and yield over time (Fry 1939; Schumacher 1961; Smith 1968; Martin and Fry 1973; Bond and Turnbull 1973; Yaremchuck 1986); altered age compositions and reductions in mean age (Martin and Fry 1973; Yaremchuck 1986); increased growth (Healey 1978b); and reduced age of maturity (Healey 1978b). Other effects, such as increased variance in some parameters (e.g. recruitment) and changes in fecundity, are mentioned in the literature (Martin and Fry 1973; Healey 1978a, b), but often are not well supported by empirical data.

The biological characteristics of lake trout (slow growth, late maturity, low reproductive potential) and the relatively unproductive nature of the oligotrophic lakes inhabited by this species (low nutrients, cold temperatures) contribute to the sensitivity of lake trout to exploitation (Olver 1988).

Types of Exploitation

In Ontario, the exploitation of lake trout generally occurs as a result of the following activities: sport fishing (angling); commercial fishing; or native subsistence fishing.

Sport fishing - Lake trout are avidly sought by anglers in Ontario. A 1985 survey of sport fishing in Ontario (OMNR and Department of Fisheries and Oceans (DFO) 1988) estimated the active angling population (adults and children) at over 3,000,000 participants. All species of trout, including lake trout, were listed as the second most popular target species group. In a recent examination of

data from a number of Ontario lake trout lakes, Goddard et al. (1987) found that on average 73% of the estimated total harvest was lake trout in lakes inhabited by lake trout and alternative sport fish.

Most of the province's 2196 extant lake trout lakes are readily accessible and have no restrictions on the number of anglers who can fish (Olver 1988). The daily catch limit in 1990 for most of southern Ontario south of approximately Lake Nipissing is two lake trout/day. In northern Ontario, daily catch limits are generally three lake trout, except for Divisions 12, 22, 24, 30, and 31, where the daily limit is two, although some exceptions do exist for individual lakes where one fish per day and size limits apply. In some lakes, slot size limits have been implemented to protect fish in the prime reproductive size categories (Division 13). Daily limits are three lake trout in all Great Lakes waters, except Big Sound and Parry Sound in Georgian Bay, which are two per day. January 1 and September 30 are the most common opening and closing date for lake trout angling seasons, although there is considerable variation in seasons between divisions. For example, Divisions 14, 24, and 25 in the extreme north have no closed season, whereas in Divisions 6, 9, and 10, and Algonquin Park (Division 13), no winter fishing is allowed.

Sport fishing for lake trout, during the winter, is popular in Ontario. The provision of open seasons for lake trout during the winter throughout most of the province in 1957 had a major impact on the growth of winter fishing (Olver 1988). Prior to 1957, winter fishing for lake trout was generally restricted to the Great Lakes, their interconnecting waterways and a few inland lakes. Only 4 yr after most of the province was opened to winter angling for lake trout, Armstrong (1961) noted that the lake trout was the species of primary interest to ice fishermen throughout the province. Armstrong (1961) cited shorter working hours, better roads, increased travel, and an increased amount of time devoted to outdoor recreation as the reasons for the growing development of the winter fishery. He also indicated the liberalization of fishing regulations played a primary role in increasing ice fishing activity on inland waters. Apparently, the general thinking of the day was that fisheries could not be overfished (C.H. Olver, OMNR, Huntsville, Ont. P0A 1K0, pers. comm.). In the Thunder Bay area, observations by Ryder (1957) indicated winter sport harvests were only about one-tenth of the open water catch. Fifteen years later, however, Ryder and Johnson (1972) noted winter anglers removed 2-4 yr of annual lake trout production from one Thunder Bay area lake in just one day.

Winter anglers have been permitted to fish with two lines throughout most of Ontario, since 1963. One line per angler is permitted during the shortened winter fishery in Division 29. Generally, winter anglers fish with few "hi-tech" aids. Still fishing with a bait fish on a single hook, or jigging with an artificial lure, often in combination with live bait, are the most commonly employed angling techniques (Clayton et al. 1984; Olver 1988).

The open water sport fishery for lake trout across most of Ontario starts at "ice out" and runs to September 30. In some cases, however, open water seasons are set by the regulations, varying from the last Saturday in April to the first Saturday in June.

Open water anglers are restricted to the use of one rod each. During the early spring, prior to thermal stratification, anglers often take lake trout near the surface while trolling with monofilament line or while trolling in shallow water with wire line. In some parts of the province, shore fishing during the early spring, either casting with artificial lures or still fishing with bait fish or pieces of sucker flesh, is popular and productive (J. Brisbane, OMNR, Chatham, Ont. N7M 5L8, pers. comm.). Later in the season, as the waters thermally stratify, trolling with steel line is the preferred method of angling (Martin and Olver 1980; McMurtry and Shuter 1985; Irwin 1989). Alternative summer angling methods that have gained localized popularity include: deep-water jigging, which became popular in Lac la Ronge in the early 1960s (Rawson 1961); and still or drift fishing, using large lake herring (*Coregonus artedii*) for bait, as noted by Clayton et al. (1984) in some eastern Ontario lakes. Although a vast array of lures are employed by lake trout anglers, an artificial lure, used in combination with bait fish, is one of the most popular lures used by anglers when trolling for lake trout (McMurtry and Shuter 1985; Irwin 1988). Olver (1988) provided an overview of the contemporary fishing gear, such as depth sounders and downriggers and pointed out that their use has increased substantially during the last 10-15 yr.

In one of the earliest analyses of winter sport fisheries for lake trout, Martin (1954) found the winter harvest exceeded that of the open water season, and that it exploited smaller, less mature fish in several Algonquin Park lakes. This occurred most often in lakes where lake trout matured at a young age (5 yr) and a small size (25.0-30.5 cm fork length (FL)). Schumacher (1961) examined four Minnesota lake trout fisheries and found winter anglers consistently caught smaller lake trout on average than summer anglers and that nearly two-thirds of the winter-caught fish were immature.

Schumacher also observed winter anglers are the first to catch each new year-class as it becomes vulnerable to fishing and thus can have a limiting effect on the summer (open water) fishery. Both Martin's and Schumacher's work pointed out to administrators that significant changes in fisheries regulations were in order. Martin's work was responsible, at least in part, for the closure of Algonquin Park lakes to winter fishing in 1955 (Olver 1988). Schumacher's work argued for a creel reduction, recognizing that this would have a much more significant effect on winter anglers than on the summer fishery. Support for these findings has been provided by numerous other workers on inland lake trout lakes across Canada (e.g. Samis 1970; Jorgensen 1973; Purych 1975; Ball 1988).

Undocumented observations of the spring and summer components of the open water fishery suggest that spring anglers are more effective than summer anglers (J. Brisbane, OMNR, pers. comm.). Martin (1970) found lake trout fed most actively during the spring months. Fry (1939) provided an early and detailed examination of the seasonal variations within the open water fishery in Algonquin Park lakes. While he noted that findings varied from lake to lake, general observations indicated that angler success (catch-per-unit-effort (CUE)) and harvest peaked in June and declined through July and August. Fry (1939) suggested that migration and feeding patterns, along with the past history of each fishery and the amount of fishing activity during the current season, influenced seasonal variations. He also noted that trout caught during the spring tended to be representative of those caught throughout the entire open water season.

The various types of angling gear used by sport anglers through the seasons tends to exploit different segments of the lake trout population. Martin (1954) noted that the winter sport fishery, which involved the extensive use of set lines and live bait, exploited a high percent of small, immature trout, while the summer angler, who typically trolled with wire line and large spoons, tended to capture larger trout. Rawson (1961) noted the deep-water jigging technique, which became a popular summer fishing technique in Lac la Ronge, accounted for the harvest of at least 70% of the trout taken from deep water, but that most of the very large trout were caught by trolling. The use of large lake herring as bait by still or drift fishing summer anglers, as described by Clayton et al. (1984), resulted in the capture of longer, heavier trout than those caught on other baits. These fish were presumably also from the older, more mature portion of the population. Olver (1988) expressed concern for the impact that the widespread use of large lake herring may have on mature brood stock. Their use or possession (alive or dead) for bait has been prohibited in divisions 9, 10, 29, and

in Algonquin Park (Division 13). The possession or use of live or dead rainbow smelt (*Osmerus mordax*) is also prohibited in Divisions 22, 24, 30, and 31.

The overview of the use of depth sounders and downriggers fishing gear provided by Olver (1988) highlights two studies that provided some insight into the use of this gear on lake trout fisheries. Duckworth (1982) noted that summer trout anglers on Lake Temagami, using depth sounders in combination with wire line, were nearly twice as successful as those using depth sounders and downriggers, wire line only, or downriggers only. Hicks (1986), using data from Lake Opeongo, found similar results, although the differences were not as marked. Hicks' data also indicated that trolling with wire line, with or without a depth sounder, is generally more successful than a downrigger, with or without a depth sounder. Both authors, however, noted that angler experience may have influenced the results. For instance, Duckworth (1982) noted that most anglers using downriggers had little experience with the device, while many anglers had several years of experience with wire line. Neither study presented data concerning whether or not the use of sounders or downriggers selected different fish than traditional summer angler methods.

There are some indications that the type of gear used by sport anglers may influence the mortality rate of trout that are caught and released. Loftus et al. (1988) examined mortality of lake trout on the Great Lakes, in a study that dealt primarily with trout caught by trolling barbed artificial lures behind downriggers. They found overall mortality among fish 46-80 cm FL was about 15%, but that mortality in fish from the smallest size range (46-51 cm) was 57.1%. Unpublished data (L. Thurston, OMNR, Parry Sound, Ont. P2A 1S4) on Georgian Bay apparently showed similar results for summer caught lake trout taken on wire line and artificial lures. Olver (1988) suggested that if mortality following release is significantly greater in smaller trout, then there may be implications for lake trout fisheries where angling methods select for smaller fish, i.e. still fishing with small bait fish on a single hook. There could also be implications in many of the province's slower growing polyphagous trout populations. For example, catch-and-release regulations may be less effective in these situations, due to post-release mortality.

Commercial fishing - In Ontario, commercial fishing for lake trout is permitted in 19 lakes, and 98.4% of the total commercial lake trout quota in the province is assigned to three lakes: Superior, Huron and Nipigon (Olver 1988). Lake trout by-catch quotas are usually equivalent to 10% of the

associated target species, lake whitefish, and do not exceed an allowable yield of 0.25 kg ha^{-1}. For example, in 1984, the Lake Nipigon whitefish quota was raised and the lake trout quota was increased, to maintain an allowable lake trout catch of 10% of the whitefish quota, but remains at well below 0.25 kg ha^{-1} (Thompson et al. 1984). The Lake Superior commercial lake trout fishery is an exception. The lake trout quota in the zone offshore from Wawa is 0.46 kg ha^{-1} and the quota in two inshore zones near Thunder Bay is 0.34 kg ha^{-1} (W. MacCallum, OMNR, Thunder Bay, Ont. P7C 5G6, pers. comm.).

Commercial fishing on smaller inland waters, such as Pettit, Eagle, and Red Lake in Atikokan, Dryden, and Red Lake districts, respectively, targets on lake whitefish, but lake trout are allowed to be harvested at 0.25 kg ha^{-1} or less (B. Ritchie, OMNR, Thunder Bay, Ont. P7C 5G6, pers. comm.).

Most commercial fisheries use gill nets with minimum mesh size and season restrictions. The majority of lake trout harvested commercially are caught by large mesh gill nets with a minimum stretched measure of 11.4 cm (4.5 in). Dates within which lake trout may be legally harvested vary considerably. In Lake Nipigon, they may be taken all year, except during the whitefish spawning period, October 15 to November 15, while on the eastern Lake Superior, the inshore fishery operates from May 5 to September 30 (B. Ritchie, OMNR, pers. comm.). On Lake Huron, there is no closed season for the commercial harvest of whitefish; however, lake trout may not be legally taken during October and November (S. Munroe, OMNR, Owen Sound, Ont. N4K 3E4, pers. comm.).

Conflicts between angling and commercial activity have increased, which has resulted in an angling lobby to curtail commercial harvesting in some lake trout waters (i.e. Inner Batchawana Bay, Michipicoten Bay, and the Montreal River all in Lake Superior; and South Bay in Lake Nipigon (native fishing only)) (MacCallum 1981; B. Ritchie, OMNR, pers. comm.).

Gillnet fisheries tend to be size-selective for the larger, older, mature segment of a population and can adversely affect the reproductive potential of a population by taking the larger, more fecund females, resulting in reduced recruitment, longevity, and yield (Colby 1984). For example, Keleher (1972) and Bond and Turnbull (1973) documented that 28 yr of commercial fishing with 13.9 cm stretch measure gill net had a pronounced effect on the fish community in Great Slave Lake. By 1974, lake trout were considered to be commercially extinct in the western end of Great Slave Lake (Bond 1974).

Most commercial fisheries have a long history of exploitation before investigations on their fish population were initiated. An exception is Great Slave Lake where studies were initiated along with the commercial fishery in 1945. Original estimates were for a maximum sustainable yield (MSY) of 1.9 million kg of whitefish and lake trout for the first 5 yr. Then the quota was doubled experimentally. Effort steadily increased 7-fold during a 20 yr period. Initially, peak catches of whitefish were associated with peak catches of lake trout, indicating that both were the result of fishing up the virgin stocks. The fishery operated from May 16 to September 25 (through the lake trout spawning period) and December to March. CUE's were relatively high for the first 5-10 yr, and then dropped drastically by 93% for lake trout and 60% for whitefish. In addition, average size of harvested whitefish and lake trout were reduced from 1.4 to 0.9 kg, and from 3.2 (east) and 4.5 (west) to 2.3 kg, respectively (Keleher 1972).

In Lake Michigan, Hile et al. (1951) noted that, although empirical data are lacking, scattered accounts indicate clearly that the largest lake trout were rare or extinct by 1927-1939. Smith (1968) presented commercial harvest figures from Lake Michigan from 1898 to 1966, which traced the collapse of lake trout and the shift in harvest to other smaller species such as alewife (*Alosa pseudoharengus*). He observed that the decline in lake trout in Lake Michigan was particularly abrupt and felt it reflected the combined effect of increased predation by sea lamprey (*Petromyzon marinus*) and exploitation by the commercial fishery.

There is some documentation to indicate that lake trout vulnerability to commercial gillnet fisheries is lower in the winter period. Keleher (1972) noted this in Great Slave Lake, and unpublished data from the Lake Nipigon commercial fishery 1980-1986 reveals the same pattern (B. Ritchie, OMNR, pers. comm.).

Harvest levels reported for commercial fisheries may be less than what is actually harvested. MacCallum (1981) found reported landings for 1978 from large mesh gill net fisheries from eastern Lake Superior were at least 35% less than actual landings. Discards and non-receipt sales were often not reported.

Native subsistence fishing - Subsistence fishing can potentially impact lake trout populations when effort is concentrated during spawning, which is when they are most efficiently harvested.

However, information is not available about the extent of this activity, or rates of harvest or impacts on lake trout stocks.

INTRODUCTIONS, INVASIONS AND LAKE TROUT STOCKING

Of the management options available to fisheries managers, species introductions are the easiest to implement, but also the one of greatest potential risk. This option normally arises when a need is perceived to establish a new species or to increase the production of a desired species. In the former case, the new species could be either an exotic or indigenous species, while in the latter case, enhancement of an indigenous species would be the objective. Our objective here is to review the effects of species introductions and invasions on lake trout populations in Ontario lakes.

As noted by Christie et al. (1972), there are differences between fish introductions and invasions. The distinction primarily relates to mode and route of entry of a species into a water body. The addition of a species into a water body resulting from direct human activities is termed an introduction. Introductions may be intentional (government sanctioned stocking; intentional but unsanctioned release by private individuals), or accidental (inadvertent fertilization and release of eggs during cleaning of catch; bait-bucket releases). Invasions result from the movement of fish from one water body to another by way of interconnecting water systems. Introductions have typically involved large, piscivorous species, while invaders have often been less desirable small fish species (Christie et al. 1972).

Much of the uncertainty associated with introduction of exotic species stems from the complex, diverse, and dynamic nature of species interactions and our relatively poor understanding of them. As a result, managing with exotics has been largely a "game of chance", as noted by Magnuson (1976). However, attempts have been made to increase the predictability of the effects of an introduction. Ryder and Kerr (1984) suggest that where introductions are unavoidable, the risks involved may be greatly reduced through a priori consideration of several ecological principles such as niche theory, interactive segregation, dominance-subordinance, and resource partitioning. Li and Moyle (1981) propose a list of four criteria that candidate species for introduction should meet. While conceding that new introductions are unlikely to meet all criteria, they suggest that "careful examination of a proposed introduction in light of such criteria should result in an evaluation of its long-term impact

on the aquatic community into which it may be inserted". Despite this possibility of reducing the associated risks, **avoidance of exotic introductions and invasions is the management strategy most often recommended by researchers, because of the great uncertainty of the effects on native species.**

Christie et al. (1972) also noted that some maintenance or restorative plantings of lake trout have effectively been introductions, because of the use of different stocks. Such supplemental stocking of lake trout threatens the genetic variability of the indigenous lake trout population and, thus, the overall fitness of the population (Krueger et al. 1981). The use of native stocks of lake trout does not totally preclude genetic related problems associated with stocking. Other potential effects of supplemental lake trout stocking, not related to genetic issues, also exist and will be discussed.

Introductions primarily affect lake trout populations through various species interactions. Perhaps the most prevalent and potentially disruptive are those associated with the food web, although behavioral, disease, genetic, and socio-economic considerations can also be important. Species interactions is somewhat of an obscure phrase that does little to identify the specific linkages between the occurrence of an introduction and an ensuing effect on lake trout populations. Often, evidence of a lake trout response is circumstantial in nature, with a change in the quantitative or qualitative characteristics of the lake trout population coinciding with increased abundance of the introduced species. The existence of other anthropogenic stressors and natural variations further compounds the difficulty of identifying causal relationships.

Introductions and invasions can be generally categorized as exotic species (fishes, invertebrates); indigenous species (fishes, invertebrates); and conspecifics (native, non-native origin). Exotic species are those not native to an ecosystem or area. Indigenous species are those that are naturally occurring in an area. These might include species that have been excluded from water bodies due to recent geological or climate events, but are otherwise naturally occurring in the area. Conspecifics refer to stocks of lake trout that are often transplanted or released into natal waters. Conspecies can be either native, that is having a common stock history, or non-native, being from another genetically discrete breeding stock.

Exotic Species

A review of the fish species introduced into the Great Lakes has been published by Emery (1985).

This chronological listing identifies 34 species of fishes that were introduced into (accidentally or intentionally), or have invaded, the Great Lakes between 1819 and 1974. Of the 34 species listed by Emery (1985), 17 are considered successful in that they have developed small to extremely large self-sustaining populations (coho salmon, *Oncorhynchus kisutch*, and chinook salmon, *O. tshawytscha*, are included in this group, even though their continued presence is largely dependent on stocking). Although the exact year of first introduction is not known for some species, all occurred prior to 1960 (Emery 1985). The most recent fish introductions are those of pink salmon (*O. gorbuscha*) in 1956 and white perch (*Morone americana*) in approximately 1950 (Johnson and Evans 1990). The river ruffe (*Gymnocephalus cernua*), a European species, has been found very recently in the St. Louis estuary of Lake Superior on the Wisconsin/Minnesota border.

While all introductions or invasions may in some way interact with lake trout, those in the Great Lakes that have received the most consideration are the sea lamprey, alewife, rainbow smelt, and the two introduced Pacific salmonids, coho and chinook salmon. Of these species, the sea lamprey has the most significant effect on lake trout being responsible in part, for the demise of that species in four of the lakes. Lamprey were first recorded in Lake Erie in 1921, became common in lakes Michigan and Huron during the 1930s and, by the 1940s, depleted populations of lake trout and some other species in lakes Huron and Michigan and eastern Lake Superior (Emery 1985). The use of lampricide and physical controls or barriers for sea lamprey control has reduced populations to about 10% of their pretreatment levels in the upper Great Lakes (Crowe 1975; Smith and Tibbles 1980).

Sea lamprey directly affect lake trout by parasitizing individuals. This frequently results in death, particularly for the smaller fish (Pycha and King 1975). The relative contribution of the sea lamprey to the subsequent demise of lake trout populations in the Great Lakes is difficult to assess, because of the concurrent existence of other stresses, including exploitation, cultural eutrophication, and the introduction or invasion of rainbow smelt and alewife (Ryder and Kerr 1984). The decreased abundance of lake trout and another large predator, the burbot, possibly contributed to the establishment of the alewife (Smith 1970) and the smelt (Christie 1974). Ryder and Kerr (1984) indicate that new steady-state conditions have not yet been attained in Lake Superior, more than 35 yr following the initial recorded invasion of the sea lamprey.

Decline in predators appears to have been a precondition for the establishment of alewife in the Great Lakes (Smith 1970). Through predation on planktivorous species and species that have planktivorous young or larvae, the alewife is thought to have caused declines in some of the most abundant prey species in these lakes: rainbow smelt; lake herring; and emerald shiner (*Notropis atherinoides*) (Ryder and Edwards 1985). The effect of alewife on lake trout was to increase growth rate and reduce age at maturity (Ryder and Edwards 1985). Alewife greatly altered and depleted the existing prey base of lake trout, but offered an alternative that was more easily consumed, as they could be found in large, dense schools (Ryder and Edwards 1985).

Ryder and Edwards (1985) indicate that it is questionable whether or not the establishment of rainbow smelt in the Great Lakes had a major diet effect on lake trout, although periods of lake trout instability may have resulted from rainbow smelt and lake herring fluctuations. These authors also noted the possibility that rainbow smelt preyed upon larval or young-of-the-year lake trout. Hatch (1984) suggested that lake trout distribution in Lake Superior appeared to have become associated with that of rainbow smelt, which is more inshore than that of the lake herring, thus reducing lake trout production compared to earlier years when lake herring formed the major diet item.

The influence that chinook and coho salmon in the Great Lakes may have on native or naturalized fish species is largely speculative (OMNR 1988a). These species may compete directly with lake trout for food items such as the alewife (Stewart et al. 1981), potentially leading to decreased growth rate of the lake trout and associated responses such as delayed sexual maturity, decreased fecundity, and increased size-dependent mortality (Hatch 1984). Conversely, Ryder and Edwards (1985) indicated that the effects of such competition may be limited due to the lake trout's greater capacity for feeding efficiently at different trophic levels. Should the primary prey (alewife) of the salmon collapse, however, they might seek alternate prey species presently utilized by lake trout, thereby having a more serious effect on the latter. The influence of pink salmon on lake trout is uncertain, due to the relatively recent nature of this introduction, but the potential for direct and indirect interaction does exist (Ryder and Edwards 1985).

The problem of introductions and invasions of exotic species also extends into the inland lake trout lakes of Ontario. The colonization of Ontario inland lakes in the Great Lakes region by the rainbow smelt is the best documented example (Evans and Loftus 1987). In recent years, smelt

appeared in three of Ontario's largest inland lakes, Simcoe, Nipissing and Nipigon in 1961, 1964 and 1976, respectively. This species is now known to occur in 194 inland lakes in Ontario (seven of these are unconfirmed reports; four may be indigenous populations; Evans and Loftus 1987). The strong association of lakes containing rainbow smelt with urban and cottage development led these researchers to conclude that introductions by humans may be the primary means of invasion and colonization by this species. Movement through interconnected waterways was identified as the probable secondary mechanism of colonization. Evans and Loftus (1987) noted that increased growth rate or change in condition factor of lake trout has been associated with rainbow smelt invasions, as has decreased growth or recruitment of juvenile lake trout. These authors present examples of rainbow smelt becoming major food sources of numerous fish species, including lake trout, in the Great Lakes and inland lakes. Increased growth was particularly evident in lakes where food items of the same size as rainbow smelt were not available. They also note that the rate of mercury accumulation in the white muscle of lake trout accelerates when lake trout switch to a diet of rainbow smelt.

Indigenous Species

Atlases of smallmouth bass (*Micropterus dolomieui*), walleye (*Stizostedion vitreum vitreum*) and muskellunge (*Esox masquinongy*) (OMNR 1988b, c, d) in Ontario have been compiled, which provide the total number of lakes containing these species and the origin of the stocks as follows:

			Introduced	
Species	Total no. of populations	Known origin	Total	In lake trout lakes
Smallmouth bass	2421	1701	823	282
Walleye	4038	3795	297	54
Muskellunge	302	268	71	19

Smallmouth bass were introduced into the Algonquin Park region in the early 1900s and subsequently invaded, or were introduced, into many other lakes within the area (Christie 1957). Ryder and Kerr (1984) indicated that physiographic barriers may have initially prevented smallmouth bass from establishing in the Hudson Bay and Algonquin Highlands, but many introduced populations now exist in these areas (Scott and Crossman 1973).

Martin and Fry (1973) stated that there is no indication that the presence of smallmouth bass in Lake Opeongo has any appreciable effect on lake trout, but bass appear to have caused a decline in brook trout (*Salvelinus fontinalis*) abundance. The apparent compatibility between lake trout and smallmouth bass is likely a function of the spatial and temporal separation of these two species (Ryder and Kerr 1984), whereas brook trout and smallmouth bass distributions overlap in the littoral zone, especially for YOY brook trout during spring. The presence of smallmouth bass may indirectly affect angling pressure on lake trout. Martin and Fry (1973) noted that the bass fishery has served to buffer fishing pressure on the lake trout, as anglers often seek smallmouth bass when angling for trout is poor. The possibility of the opposite occurring is limited, as bass fishermen are unlikely to angle for lake trout (Martin and Fry 1973).

K.E. Coleman (OMNR, Kemptville, Ont. K0G 1J0, pers. comm.) indicated that Tweed District has a number of lakes in which the lake trout became extinct following walleye introductions and development of strong walleye fisheries (lakes Skootamatta, Mississagagon, Buckshot, and Fortune). He suggested that the degree of interaction between walleye and lake trout may be related to lake size. Large lakes may afford sufficient spatial separation between these two species to minimize interactions. In smaller lakes having limited lake trout habitat, interaction with walleye would be expected to be stronger.

Lake herring were first introduced into Lake Opeongo in 1940 and later in 1948 (Martin and Fry 1973). They were first identified in lake trout stomachs in the early 1950s and, by 1973, became the most abundant species in the lake (Martin and Fry 1973). Lake herring were also introduced to Crystal Lake (Kirkland Lake District), and the Mishibishu lakes (Wawa District), but effects have not been documented. The origin of lake herring in most districts is not well known, and generally the level of concern over this species as a stressor on lake trout is low (Lewis et al. 1990). The effects of the lake herring introduction on lake trout have been well documented for Lake Opeongo (Martin 1970; Martin and Fry 1973; Ryder and Kerr 1984). Lake trout responded to this new forage item with increased growth rate as well as increased ovary weight, egg size, and egg number. There was also a decrease in the percentage of infertile adult lake trout (Martin and Fry 1973). Accompanying these changes was a trend to later maturity. Overall, this introduction resulted in greater lake trout productivity, initially through increased growth and later by contributing towards greater recruitment, as a result of increased fecundity (Matuszek et al. 1990). Lake herring may also compete with young

lake trout for zooplankton (Ryder and Kerr 1984), and larvae and fry of lake trout may be vulnerable to predation by the herring in the late winter (Martin and Fry 1973), but this effect, if present, is counteracted by the above benefits.

Other species that have invaded or been introduced into lake trout lakes in Ontario include yellow perch, rock bass (*Ambloplites rupestris*), and splake (Lewis et al. 1990). Evidence of effects of these species on lake trout does not presently exist.

Recent studies of the influence of fish community structure on lake trout yields suggest that some indigenous fish species might limit lake trout production. Lake whitefish and burbot (Goddard et al. 1987; Carl et al. 1990) and walleye, as noted, are the species of primary concern in this regard, although several others, including most notably round whitefish and mottled sculpin (*Cottus bairdi*), are known to be predators of lake trout eggs and fry (Stauffer and Wagner 1979; Hassinger and Close 1984; Hindley 1984).

Invertebrates

Crayfish, *Orconectes virilis* and *O. propinquus*, are known predators of lake trout eggs (Horns and Magnuson 1981). Horns and Magnuson (1981) found some evidence of differential predation rates on lake trout eggs by *O. virilis* and *O. propinquus*, depending on substrate type. Eggs on sandy substrate were more vulnerable to predation by *O. propinquus*, but were equally vulnerable to both crayfish species when on rocky substrate. Both *O. propinquus* and *O. virilis* occur in Ontario, but their influence on lake trout populations is unknown. There is clearly a potential risk in introducing these, and possibly other species of crayfish, into lake trout lakes.

Mysis relicta has been introduced into lakes in British Columbia, the United States, and Scandinavia (Lasenby et al. 1986). These introductions were conducted in order to establish a supplementary food source for fish. In many instances, this species has become established in many water bodies downstream of the initial introduction (Lasenby et al. 1986). In Ontario, *M. relicta* distribution is related to glacial history, with no evidence of intentional introductions into a water body (Ricker 1959; Martin and Chapman 1965; Dadswell 1974). D. Lasenby (Trent University, Peterborough, Ont. K9J 7B8, pers. comm.) also indicated that intentional or accidental introductions of *M. relicta* have not occurred in Ontario.

Lasenby et al. (1986) provided a review of the effects of *M. relicta* introductions on fish communities. The effects of these introductions often are conflicting and include: enhanced growth and survival of lake trout; decline in abundance of several species of cladocerans, with resulting decreased abundance of pelagic fish species which normally feed on these (and do not switch to a diet of *M. relicta*); and increased growth rate and size at maturity of some Kootenay Lake kokanee (*O. nerka*). These authors concluded that there was little evidence that *M. relicta* introductions are a positive long-term management practice and recommend that, until the probable impact of such introductions can be assessed, a moratorium should be imposed on further management introductions of *M. relicta*.

The brackish-water copepod *Eurytemore affinis* and the cladoceran *Bythotrephes cederstroemi* are relatively recent Great Lake introductions whose effects are not yet known (Ryder and Edwards 1985). Also, the zebra mussel (*Dreissena polymorpha*) was first recorded in Lake St. Clair in 1988 and has since established populations in Lake St. Clair and Lake Erie. Establishment of populations in Lake Ontario and some inland lakes appears inevitable. A review of European experiences with the zebra mussel and some discussion of possible implications for North America is provided by the Ontario Ministry of the Environment (OMOE) (1989).

Supplemental Lake Trout Stocking

Results from the lake trout questionnaire (Lewis et al. 1990) indicate that there are 269 lakes in Ontario that contain native, reproducing lake trout which also receive supplemental stocking of non-native lake trout (status code N3, Table 1). This represents 14.7% of the 1827 lakes in the atlas which contain native lake trout.

There are considerable differences between regions in the occurrence of this stocking practice. For example, in the Eastern Region, 35 of the 61 native lake trout lakes (57.3%) are in this category. In the Northwestern Region, this is the case for only two of the 515 lake trout lakes (0.4%). These geographic differences are related to the distances of the lakes from centers of high human population density. Supplemental lake trout stocking is discussed in more detail in a companion report (Evans et al. 1991).

Interactions Involving Introductions and Other Stressors

Much of the previous discussion has focused on the impact of introductions and/or invasions on lake trout populations without consideration of other stressors that may be acting on the population simultaneously. Concurrent stressors may combine to alter the nature and magnitude of the impact on lake trout, or they may interact to produce a lake trout response that might not occur in the presence of each stressor in isolation. Two examples of such interactions considered are: introduction of rainbow smelt and the presence of mercury (Hg) contamination; and supplemental stocking of hatchery lake trout and exploitation.

Effect of rainbow smelt introductions on the uptake of mercury by lake trout - Evidence from several published studies indicates that the presence of rainbow smelt in the diet of the lake trout contributes to elevated concentrations of Hg in lake trout. Akeilaszek and Haines (1981) found that lake trout in two northern Maine lakes containing rainbow smelt had a higher rate of mercury uptake with increasing length than did lake trout in a nearby lake where rainbow smelt were absent. MacCrimmon et al. (1983) observed an abrupt increase in the rate of mercury accumulation in lake trout, following a change in diet from benthic invertebrates to rainbow smelt in Tadenac Lake, Ontario. These authors also found a strong correlation between mercury levels in smelt and trout calculated at standardized length in nine inland Ontario lakes ($r = 0.96$, $P < 0.01$). An increase in the amount of smelt in the diet has been shown to increase mercury accumulation in species other than lake trout, for example in walleye and in northern pike (*Esox lucius*) (Mathers and Johansen 1985). The explanation generally accepted for these results is that smelt accumulate higher concentrations of Hg than do other forage species, as Mathers and Johansen (1985) have shown for Lake Simcoe.

Data from the "*Guide to Eating Ontario Sport Fish*" (OMOE and OMNR 1988) also indicate that smelt can influence mercury accumulation in lake trout (Evans and Loftus 1978). The percentage of lakes with concentrations of Hg in lake trout exceeding 1.5 $\mu g\ g^{-1}$ (wet weight) were compiled over a series of length classes for lakes containing lake trout only, and for lakes containing both lake trout and rainbow smelt. Over the range of FL classes considered (from 20-25 cm to >75 cm), the percentage of lakes with high Hg concentrations in lake trout was greater for the group of lakes with smelt present than for the group with smelt absent.

Further evidence that consumption of smelt by lake trout may lead to elevated Hg levels is provided by a data set on 91 Ontario lake trout lakes (described by McMurtry et al. 1989) for which there was a significant linear relationship between log Hg concentration in lake trout and total length. McMurtry et al. (1989) had found that dissolved organic carbon in lake water was the only lake descriptor significant in predicting values of log Hg in lake trout using a step-wise regression procedure on this same lake set. However, when smelt was added as a "dummy" variable to the equation (absence coded as 0, presence coded as 1), it was also significant (partial $r^2 = 0.05$, $P < 0.03$).

In summary, there is little doubt that the presence of smelt in the diet of lake trout can contribute to increased concentrations of Hg in the flesh of lake trout. The quantitative nature of this relationship has not yet been described, but it is known that there is a positive correlation between Hg concentration in smelt and Hg concentration in lake trout. Therefore, in lakes with relatively little Hg present in smelt (or available to be taken up by smelt), the presence of smelt will probably not contribute to unacceptable levels of Hg in lake trout. For example, in Lake Simcoe, the average Hg concentration in smelt and lake trout reported by MacCrimmon et al. (1983) was 0.08 $\mu g\ g^{-1}$ and 0.39 $\mu g\ g^{-1}$, while in Vernon Lake, the mean concentration in smelt was 9.45 $\mu g\ g^{-1}$ and the concentration in lake trout was 4.49 $\mu g\ g^{-1}$.

Supplemental stocking of hatchery-reared lake trout and high exploitation - Supplemental stocking of lake trout is a common practice where native stocks have been depleted by excessive exploitation and/or by the effects of other stresses acting on recruitment success. Stocking of hatchery fish will almost always contribute to angling harvest and, in many cases, will tend to stimulate fishing pressure. Supplemental stocking, in these cases, will tend to not only counteract attempts to maintain or enhance the native stock, but might actually accelerate its decline. If, for example, the exploitation rate exceeds the natural replacement rate of the wild fish, but not the stocking replacement rate of the hatchery fish, the latter will soon replace the former. The time trajectory of such displacement will depend on the actual mortality rates of both stocks as well as their reproductive behaviour and success. The effects of stocking hatchery-reared lake trout are addressed in detail by Evans et al. (1991). They used a computer simulation model to illustrate the magnitude and time course of changes in the abundance of wild lake trout subjected to stocking and exploitation. The combined effects of exploitation and stocking were found to suppress the wild fish and to ultimately lead to their extinction.

HABITAT MODIFICATIONS

Description of Physical Habitat

It is essential to understand the physical habitat requirements of lake trout, in order to appreciate the effects of various stressors. Habitat requirements differ markedly for the various life stages of lake trout and are reviewed here accordingly.

Spawning habitat - In Ontario, lake trout spawn in water temperatures ranging from 8.9-13.9°C (Scott and Crossman 1973), although water temperature alone does not initiate spawning. For the most part, spawning occurs over cobble-gravel substrates, which are devoid of infilling material and which are composed of materials between 5 and 20 cm in diameter (a 10 cm particle-size is likely about optimum) (Sly 1988). In most inland lakes, spawning occurs over cobbles 2.5 cm or larger in diameter (Merriman 1939; Hacker 1956; DeRoche 1969; Martin and Olver 1980). Boraski (1983) observed reproductive success in Devil Lake on substrate that was gently sloping, composed of cobbles and boulders of 25-50 cm diameter, containing numerous deep interstices that were free of silt. The structure of the gravel is important because the interstitial spaces must be capable of entrapping lake trout eggs and, at the same time, excluding predators (Sly 1986). In Ontario, there are four main types of cobble-gravel: beach deposits, channel deposits, scree or talus deposits, and lag deposits (Sly 1986). In addition, any of these may be relict (formed at a previous time and now submerged) or modern features. Substrates of silt, clay, or marl are generally unsuitable for successful reproduction (Marcus et al. 1984).

The development of lake trout eggs requires a stable substrate. Therefore, it is unusual for these eggs to be deposited in actively forming or moving beach or channel gravels (Sly and Schneider 1984). It is likely, however, where such materials are no longer active (i.e. moving), that they will provide an excellent substrate for spawning fish if the sites are not subject to infilling particulates (Sly and Widmer 1984; Sly 1988). Beach and channel deposits tend to be of relatively large size, typically hundreds of square meters in usable area. Such deposits, however, are rarely available as relict geological deposits with the right combinations of water depth and lack of infilling.

Scree deposits form against steep bedrock outcrops where sub-aerial weathering processes (both freeze-thaw and solar heating) cause fracture and separation of material from the rock face (Sly

1986). Scree deposits are of wide occurrence and where they are composed of resistant material and where these deposits are now covered by water, it is likely that they will be subject to little erosion, except the removal of fine particulates in response to wave-wash and current motion. Scree slides are gravity driven phenomena and typically they are composed of very large boulders toward the base of the deposit, with materials becoming finer up the face of the slide. Particle size distributions are patchy in scree deposits, and it is possible for specific size materials to provide suitable spawning substrates at a number of different elevations across the surface of the scree slide, but rarely in patches more than a few meters or tens of meters in area.

Lag gravels can be formed in many ways, but in Ontario, the most common form is as a residual deposit of coarse particulates which has been left after erosion of fine sand, silts and clays from glacial tills. Lag gravels may cover very large areas (some areas can be measured in square km). Coarse materials usually occur as discrete clumps, interspersed with larger areas of finer material. Suitable cobble-gravel substrates are associated with the clumps of coarse material where they tend to be present as small patches (usually a few tens of square meters in extent). The distribution of clumps may be random but, more often, it is not. Residual deposits derived from glacial materials frequently retain linear elements associated with the original formative process (P.G. Sly, Rawson Academy, Ottawa, Ont. K1N 7B7, pers. comm.).

Egg penetration in cobble-gravel deposits depends on the size of the interstitial spaces and the uniformity of the particle size. In the finest size of cobble-gravel, eggs may not penetrate the first layer of particulate material, and will be directly exposed to surface predation and siltation. In cobble-gravels (mean size 5-10 cm diameter), where interstices are not much larger than the size of lake trout eggs, little penetration beneath the first layer of particles is likely. This is because of the combined effects of lodgement and egg swelling which takes place shortly after spawning. The internal structures of beach, lag and talus deposits, however, may differ significantly, and could result in very different egg penetration depths. Beach deposits respond to seasonal fluctuations of water level and wind/wave energy. Because of this, increased wave activity in the fall can result in the formation of a coarse cobble-gravel surface layer which overlies finer (summer, or entrained) material. Thus, egg penetration in such deposits is likely to be very limited. Lag deposits, however, are formed by processes which remove fine particulates from composite materials, leaving behind a residue of very coarse material. The more intense are the erosional processes (typically due to wave action),

the coarser the residue. However, residual materials quickly provide a protective armoring and the thickness of such lag deposits is usually limited to a few layers of coarse particulates. The effects of winter ice movement may locally increase the depth of such deposits. In very coarse aggregates, eggs may penetrate as deep as the interface of original material (perhaps as much as 0.2 to 0.5 m (Sly 1986). Talus materials, on the other hand, are characterized by great variations in particle size and structural form, and egg penetration is likely to be equally variable. Unfortunately, no data are available to indicate the percentage of eggs which penetrate successively deeper into various spawning substrates (Sly 1986)).

Observations reported in the literature suggests that, in many cases, spawning appears to be associated with very logical and site-specific conditions; but, in other cases, a degree of opportunism appears to exist which may allow successful spawning at alternative sites. Spawning depths in North American lakes have been reported to range from 15 cm to more than 55 m (Merriman 1939; Carlander 1969; DeRoche 1969; Johnson 1975), and possibly to greater depths in the Great Lakes (Eschmeyer 1954; Scott and Crossman 1973). Studies on spawning lake trout in Seneca and Cayuga lakes of the New York State Finger Lakes region (Royce 1951), lakes Michigan and Superior (Eschmeyer 1954; Organ et al. 1978) and other Great Lakes (Coberly and Horrall 1980; Goodyear et al. 1982) have indicated lake trout spawning at very shallow depths (<2 m) and to a maximum depth of more than 90 m. In a survey of 221 confirmed lake trout spawning sites in 82 inland Ontario lakes, McMurtry (1986) determined that 78% (172) were located in water with a mean depth of less than 2 m and as shallow as 30-40 cm.

Early life habitat - The eggs remain within the substrate for many weeks. Hatching time for eggs increases with decreasing temperatures (Embody 1934; Carlander 1969): approximately 50 d at 10°C, 100-117 d at 5°C; and 141-156 d at 2-2.5°C. Martin (1956) determined incubation periods for a number of Algonquin Park lakes and observed that, although spawning occurred in mid- to late-October, hatching varied from February 15 to March 30 (15-21 wk).

Fry voluntarily leave the spawning substrate during the swim-up stage (Wilton 1985). In lakes Louisa and Opeongo, Ontario, no young lake trout were captured in fry emergence traps prior to May 2, 1979 (Anon. 1980). Peak emergence in Lake Louisa was about May 15, and about May 23 in Lake Opeongo. These observations suggest that lake trout emerge from the gravel when surface

water temperatures reach 8-10°C. In Devil Lake, Ontario, Boraski (1983) caught emergent fry from April 26 to May 15. When the last of the fry were captured, the water temperature was again between 8-10°C.

After emergence, the young trout usually seek deeper water. Little is published about the habitat and behaviour of juvenile lake trout, but almost certainly they go to depths to avoid potential predators (Evans et al. 1991). Studies in the upper Great Lakes suggest that, during early to mid-summer, young lake trout may inhabit sandy plains, which are largely devoid of competitor or predator species (Peck 1982). In general, juvenile lake trout are found at greater depths than adults during summer (Evans et al. 1991). DeRoche (1969) found YOY lake trout in the littoral zone in early spring, but the young trout moved to 25-50 m within a few days after surface temperature reached 8-10°C.

Adult habitat - In the autumn, usually in early October, adult lake trout in small lakes tend to move inshore to the rocky shallows in preparation for spawning. After spawning is completed, they disperse freely throughout the lake at various depths, and remain dispersed throughout the winter months (Scott and Crossman 1973). In spring, they often occur in surface waters immediately after ice break-up. As surface waters warm, with the advance of spring, lake trout seek cooler waters, eventually retreating to the hypolimnion during the warmer summer months. The depth of the thermocline in any particular lake depends on many factors, such as latitude, size of lake, watershed elevation, flushing rate, height of surrounding land (hence, protection from wind), and fetch (Shuter et al. 1983). In most small lakes, the thermocline occurs at depths of 12.0-18.0 m. Lake trout can make excursions above the thermocline, usually to feed, despite unfavourably warm temperatures (Scott and Crossman 1973). During summer, the preferred water temperature stratum is 8-12°C and has at least 6 ppm oxygen (Marcus et al. 1984), although a wider range of temperatures (6-13°C) is normally frequented (Martin and Olver 1980; Evans et al. 1991).

Stressors of the Physical Habitat of Lake Trout

Many types of aquatic habitat modification are known to have a significant impact on lake trout reproduction (Machniak 1975). Some shoreline modifications may affect water quality, reducing oxygen in the hypolimnion and, thereby, reducing the preferred habitat available to lake trout in the lake. There is little evidence, however, that substrate modifications affecting the physical habitat have

seriously impacted survival and growth of lake trout after they have reached a late stage of juvenile development.

The following alterations of the physical habitat of lake trout are discussed below: shoreline modifications; substrate extraction; dredged material disposal; and water level modifications.

Shoreline modifications - Lake trout tend to spawn on exposed shorelines or in tributaries over coarse substrate, which would indicate that there is great potential for shoreline modifications to affect the spawning habitat of lake trout. Shoreline modifications, including infilling of bays, the construction of solid berms and jetties, or the formation of new water bodies by excavation or partial closure, changes in the types of material which form the shoreline involving the use of coarse materials, blocks or pilings to protect shorelines, and placement of sand over other types of substrate to create beach areas can significantly effect the well being of lake trout populations. In addition to massive loss or transformation of littoral habitat, concern also derives from the spread of organic matter and fine particulates (inorganic), disturbed during construction activities, such as road construction, timber extraction, mining, and land clearing for development. Inorganic material, such as fine particulates, may reduce embryo survival by clogging the interstitial spaces in spawning substrates (as noted for lake trout and other species: Johnson 1961; Carlson and Sieffert 1974; Reiser and Bjornn 1979; Gaboury 1985). This effect may occur at some distance from the point of disturbance. It is also possible that changes in shorelines can alter local patterns of wave approach or current flow, and that these too may result in the long-term accumulation of fine particulate and organic material in areas formerly swept clean, or distant from the transport of fine particulates. Organic matter, in addition to clogging the interstitial spaces, can decompose and result in oxygen loss or elevated ammonia within the substrate. In severe cases, oxygen can be depleted to a level insufficient for the developing embryos to survive (Sly 1988). Plant and algal debris can be trapped and accumulate in the substrate of spawning sites where there are high nutrient levels originating from shoreline disturbances. Also, shoreline modification may indirectly influence lake trout, by affecting the abundance and diversity of their prey and egg predators.

There is a lack of published documentation to confirm what, if any, indirect impacts there may be, or if these impacts are positive or negative. There is also a lack of published documentation recording shoreline modification problems specific to lake trout; although it seems likely that some

such problems do occur in inland lakes (resulting in the loss of small, but perhaps important, areas of lake trout spawning habitat). On the other hand, there are published observations which record that coarse aggregates (often used for erosion control or as construction materials) may be used as artificial spawning substrates by lake trout (Martin 1955; Prevost 1957; Peck 1982; Sly and Schneider 1984). Thus, shoreline modifications can result in either deleterious or beneficial changes for spawning lake trout, depending largely upon materials used and site exposure.

Substrate extraction - Substrate extraction is conducted by the construction industry for the recovery of sands, sandy gravels and gravels. Smaller quantities of substrate, also, may be removed during the preparation of foundations for large bottom-mounted structures in lakes and tributaries (e.g. bridge footings, dams and hydro plants). Because of the high costs of underwater aggregate recovery, sand and gravel extraction is generally done only where suitable deposits exist near large markets and, thus in most cases, commercial extraction is not undertaken in inland lakes. Aggregate recovery occurs at a number of sites in the Great Lakes (Department of Public Works 1975), but there seem to be no well documented studies specifically reporting deleterious effects on lake trout spawning sites. Almost certainly, however, such problems have occurred in the Great Lakes and elsewhere, but there is no substantive evidence. Historically, aggregate removal commonly occurred in Lake Ontario from about 1830 to the early 1900s (W.J. Christie, OMNR, Picton, Ont. K0K 2T0, pers. comm.), but the effects, if any, on lake trout of this activity are not documented. In addition, there have been instances where local property owners have used adjacent aggregate materials to protect or enhance shoreline property but, again, there is virtually no documented evidence that such actions have impacted on lake trout spawning sites in inland lakes. As with the effects of shoreline modification, the dispersal of fines or modifications to local water motions caused by substrate extraction also pose a potential problem to adjacent spawning sites.

Disposal of dredged material - Materials are usually removed by dredging to maintain or create navigation channels in shallow, nearshore areas, often bays or at the mouth of tributaries, or in connecting channels. Maintenance dredging is usually concerned with the removal and disposal of fine silty materials. Often, these materials contain elevated concentrations of some contaminant materials derived from nearby urban or industrial sources, or from agricultural runoff (Ryder and Johnson 1972; PLUARG 1978; Ryder and Edwards 1985). Typical contaminants include nutrients (bio-available compounds of P, N, and C), heavy metals, oils and greases, phenols, PCB's, and the

more persistent pesticides. Disposal of these materials may pose two major problems for lake trout spawning sites. First, disposal of fine particulates from either dredging or disposal sites may (as previously noted) result in entrapment of fines or degrading organic matter, in otherwise clean cobble-gravel substrates. If these substrates are below depths affected by wave motion, or are in areas no longer subject to strong current motion, the fines cannot be removed by natural process and the availability of such sites as spawning habitat will be lost. Second, the presence of contaminants may prove detrimental to the development of embryos held in coarse substrates, following the spawning of lake trout. In the Great Lakes and throughout Ontario, strict water quality guidelines (International Joint Commission (IJC) 1978) limit the presence of contaminants to very low levels (in materials approved for open water disposal) and protective measures are required where the loss of fines at dredging sites could present a potential contaminant hazard.

As long as requisite controls on the loss of fines (at both dredging and disposal sites) and their contaminant content are adhered to, dredging poses little concern with respect to the long-term quality of existing lake trout spawning sites. Where such safeguards are lacking or not applied consistently, there is a real possibility of damage to spawning habitat. There appears to be little or no documentation of lake trout spawning habitat loss, due to dredging or disposal of dredged material. On the contrary, where new channels or greater lake bed deepening is required, it is often necessary to remove fractured rock or coarse aggregate materials. Such materials have been used for adjacent shore protection or construction, or disposed of in adjacent waters. If properly sized and distributed, these materials can form attractant reefs and may, under ideal conditions, form artificial lake trout spawning sites (Martin 1955; Peck 1982).

Water level modifications - Water level changes generally follow one of two main patterns: changes due to raising or lowering of the outlet elevation (such as by a solid weir); or major manipulations of water level by draw-down or recharge control. In the first case, although minimum and mean water levels are changed a little, the natural variation about the mean (water level regime) is least affected and may closely parallel the original cycle prior to alterations at the lake site. In the second case, mean water levels are likely to differ considerably from those of the natural lake but, more particularly, draw-down and recharge may result in lake level fluctuations which, in no way, follow a natural regime (both in terms of periodicity and the actual level of the water surface). Commensurate with extreme changes, there may be problems associated with discharge immediately

below an impoundment, including alterations to water temperature and various water quality parameters (such as dissolved gases).

Generally, permanent water level changes, as in the case of a weir, result in minor changes of water level, not unlike natural changes such as would be caused by beaver dams. Usually, there is sufficient spawning substrate to allow a shift in habitat use to an alternative and often adjacent site. This would be especially important in situations where the previously used sites become unsuitable as a result of material infilling or less commonly, site exposure. There may be situations where a permanent increase in water levels can result in the availability of additional spawning substrate and actually be beneficial to spawning lake trout.

There is little likelihood that minor changes in water level will have significant impact on the availability of thermal habitat for adult lake trout. Concern about water level regulation is primarily related to availability of suitable spawning and nursery habitat, but negative effects on summer habitat of whitefish and cisco have been reported (Gaboury and Patalas 1984).

The concerns imposed by water level control structures that can be manipulated, i.e. stop logs, are much greater (Machniak 1975). Wilton (1985) examined three lake trout lakes in the Madawaska-Muskoka region of Ontario, two of which experienced water draw-down. Bark Lake experienced an extreme winter draw-down of 10 m and it was determined that the draw-down exposed all of the potential spawning shoals and resulted in a complete loss of reproduction. Data and observations from Mary Lake indicated that natural reproduction of lake trout may be severely curtailed at one of two shoals, due to a winter draw-down of as much as 0.8 m. Wilton (1985) also concluded that sac fry will not swim prior to the swim-up fry stage, and the occurrence of suitable water temperatures of 8-10°C (Anon. 1980; Wilton 1985). This means that eggs and young lake trout will be most vulnerable to draw-downs from early October to mid-May on most lakes in the Algonquin and Eastern regions (Boraski 1983; Wilton 1985), and quite likely over most of Ontario, depending on the depth at which they spawn. In Maine, DeRoche (1969) found that lake trout spawned in Thompson Lake and Cold Stream Pond at water depths ranging from 0.2-1.2 m, but that most spawning occurred at depths of about 0.3 m. He maintained that a draw-down of as little as 0.3 m, occurring after lake trout spawning, could cause very high egg loss. An evaluation of lake trout egg deposition on 14 spawning shoals in Lake of Bays, Ontario, revealed that 28% of the eggs were

deposited at depths of less than 1.0 m (Anonymous 1988). A winter drawdown of 1 m, therefore, would result in a minimum of 28% mortality of the total egg deposition.

Gunn (1987) found that early life stages of lake trout can detect increased levels of acidity, however, they did not avoid acid waters by swimming further down into the substrate. It appears that developing lake trout either are unable to or will not move from their position in the substrate until they develop to the swim-up fry stage, which does not appear to occur until the surface water temperatures reach 8-10°C.

There are many lake trout lakes throughout Ontario in which overwinter draw-down would be sufficient to expose most available spawning substrates, thereby causing total mortality of eggs deposited on these sites. Conversely, recharge may be sufficient to drown spawning habitat beneath much greater than normal water depths. However, in Lake Minnewanka, Alberta, this did not appear to inhibit continued use of original spawning habitat by local stocks of lake trout (Currier and Schultz 1954). In most cases, however, such substrate would become unusable because of long-term infilling by fine particulates (P.G. Sly, Rawson Academy, pers. comm.).

Major changes in water level or water flow regimes may influence not only spawning and nursery habitats, but also the thermal habitats of juvenile and adult fish. If the volume of cold water is reduced as a result of drawdown, it is possible that the required cold-water habitat is only available at depths which are subject to dissolved oxygen depletion (Ryder and Edwards 1985). Under these conditions, available habitat may no longer support lake trout at any point in their life history.

Water level fluctuations may also indirectly affect lake trout populations. Winter draw-downs, for example, may also eliminate production of lake herring and lake whitefish, depending on the depth at which they spawn. The lake herring, in particular, is an important prey for lake trout, in lakes where they co-exist. The loss of any prey species quite likely would result in a lower lake trout production (Matuszek et al. 1990).

Because water level changes involve lake-wide, as opposed to site-specific, habitat modifications, effects due to water level change are generally of greater significance than other types of habitat modification. Further, there are uncertainties which relate to the response seen in fish behaviour.

Some wild stocks and some introduced stocks of lake trout seem to be able to adapt and make use of alternative spawning sites in lakes. Other stocks do not adapt and continue to use original natal substrates, despite the fact that they may no longer provide adequate spawning habitat (Sly and Widmer 1984). Some stocks appear to be incapable of selecting new spawning habitat with resulting recruitment failure. It is not known what factors control the ability of lake trout stocks to adapt to new spawning sites, though the presence or absence of other stressors (including fishing pressure) may be significant.

WATERSHED MODIFICATIONS

Many human activities on a watershed can indirectly affect lake trout through their influences on allochthanous material inputs and hydrology and, in turn, on lake habitats. These activities include: road building, including stream crossings; construction and development; logging and other forest management activities; agricultural practices, including drainage; dam construction and operation; and fire. This discussion will be restricted to an evaluation of the above activities, which occur, for the most part, in a watershed rather than in a specific lake environment.

Evaluation of Stressors and Impacts

Road building - The construction of roads and their associated stream crossings results in two primary concerns: inputs of silt and sediment, and inputs of salts to streams and lakes. Silt and sediment inputs are of concern because of their tendency to clog interstitial spaces in rock substrate. This can lead to reduced oxygen levels in the substrate, and subsequent egg mortality if the substrate is used by lake trout for spawning. In addition, there may be effects on organisms important as lake trout prey (mayflies, for example). There is good evidence for increased inputs of sediments from forest road construction (including stream crossings) (Anderson 1970; Mattice 1977; Englert et al. 1982; Plamondon et al. 1982) and highway construction (Mathers 1978). Although most studies documented increased inputs to streams, we can presume inputs to lakes (either directly or via stream flow) are also increased. There is also good evidence that the presence of fine sediments in spawning gravel reduces egg survival of several fish species (Johnson 1961; Reiser and Bjornn 1979; Gaboury 1985). Hindley (1984) found that lake trout eggs in laboratory experiments could not survive in 5 mm of silt. The impacts of sedimentation on incubating lake trout embryos in the field will be dependent on the spatial and temporal pattern of sediment transport and deposition, relative to the location and timing of lake trout spawning. These factors will vary from case to case.

Inputs of salt from roads may be of concern, if concentrations cause osmoregulatory stress in fish. Sodium chloride, used in southern Ontario for de-icing roads in winter, and calcium chloride, used as a dust inhibitor in summer, are likely carried from roads into adjacent streams and lakes (Ryder and Johnson 1972). In the Yahara Lakes, Wisconsin, sodium and chloride concentrations have increased since the use of road salt became common in the 1960s (Lathrop 1988). However, current levels are 10-times below the levels considered to be toxic to freshwater organisms and, at current rates of increase, are not predicted to cause concern in the foreseeable future. Effects on lake trout in Ontario are unknown but, based on the Wisconsin experience, we suggest such effects are minimal at most.

Construction and development - Most of the impacts from activity of this nature relate to the addition of silt and nutrients from land-clearing, construction of roads, and storm sewers, etc. The construction of seasonal and year-round residences can produce marked changes to the terrestrial environment along lake shorelines, thereby affecting adjacent aquatic habitats. The concerns are similar to those related to logging. Removal of vegetation and disturbance of the soil by heavy machinery can cause shoreline erosion and associated inputs of silt and nutrients (Darnell 1976). Brugam (1978) found that sedimentation rates in Linsley Pond, Connecticut, increased when cottages and homes were built in the watershed. Accelerated erosion and siltation were reported by Anthony and Jorgensen (1977) on Lake Nipissing, as a result of watershed urbanization and recreational shoreline development. In addition to causing increased turbidity and silt deposition, erosion from shoreline development activities can result in increased nutrient loadings. Sonzogni et al. (1977) estimated that shoreline erosion contributes about 25% of the total phosphorus loading to the Great Lakes, indicating the significant influence of shoreline disturbance. Samsel (1973) also found increases in N, P, and Si concentrations following erosion from lakeshore home construction.

In two relatively undeveloped Ontario lakes, Jerry (50.1 ha) and Red Chalk (56.9 ha), Dillon et al. (1986) found that 81% and 51% of the total phosphorus input was from streams and runoff. Atmospheric deposition provided the balance of the total phosphorus loadings. The same two authors found that two other small lakes, Dickie and Harp, had their annual total phosphorus loads increased by 2-fold, as a result of shoreline cottage development.

Forest management practices (exclusive of road building) - Forest management operations, including harvest, utilization, removal and scarification, can result in increased sediment and nutrient inputs to lakes, directly and indirectly via streams. Numerous references in the literature indicate that these activities result in increased sediment inputs, but the magnitude of this effect is not well documented (McNamee et al. 1987). Most of the studies were conducted in mountainous areas (Lull and Sopper 1969; Bormann et al. 1974), and the effects were measured in streams. One northwestern Ontario study indicated little erosion, 1 and 2 yr after clearcutting (Nicholson et al. 1982). There is good evidence that sediment export from these types of forest management activities other than roads is substantially less than from road-related activities (Anderson 1970; McCashion and Rice 1983).

The other area of concern related to forest management is nutrient loading. There is evidence of increased phosphorus exports in studies of the boreal forest in northwestern Ontario (Nicholson et al. 1982) and similar forest type in New Hampshire (Bormann et al. 1974). However, McNamee et al. (1987) indicated that these inputs are unlikely to influence lake phosphorus concentrations, due to the generally greater water export resulting from clearcutting and the unavailability of much of the phosphorus (organic or mineral-bound) under well-oxygenated conditions. In systems where anoxic conditions naturally occur, or are stimulated by organic matter inputs, the impacts of forest management-related increases in phosphorus would be expected to be greater. These influences could include increased primary productivity and decreased hypolimnetic oxygen. Effects on lake trout may include reduced egg survival (algal growth on shoals) and decreased summer habitat (hypolimnetic volume), although direct evidence of these types of effects is not available.

Agriculture - Agricultural practices can result in increased loadings of nutrients, silt, metals (Johnson and Nicholls 1988, 1989), and pesticides (insecticides, herbicides, fungicides) (Frank et al. 1978). Nutrient loading problems result primarily from the application of liquid and dry fertilizers. The effects on lake trout can be via two pathways: (1) deterioration of spawning shoals through algal growth, resulting in elevated ammonia, decreased interstitial oxygen, and decreased egg survival (Sly 1988); and (2) decreased hypolimnetic oxygen, resulting in diminished summer habitat for lake trout (Ryder and Johnson 1972; Evans et al. 1991). An increase in nutrient loading has been witnessed in Loch Lomond, U.K., as a direct result of increases in application of fertilizers for agriculture (Maitland 1972).

Silt inputs can also be increased as a result of agriculture practices. Silt eroding from farmland can be deposited on spawning beds, resulting in decreased egg survival (Ryder and Johnson 1972). In Rondeau Bay, Lake Erie, major water quality and fish community changes have resulted from erosion of the surrounding watershed, which is under intensive agriculture (OMNR 1985). In Lake Simcoe, the demise of the lake trout stock has been attributed, in part, to recruitment failure caused by siltation of spawning beds (Hindley 1984). Intensive agriculture on the Lake Simcoe watershed may account for a significant amount of this siltation effect (Johnson and Nicholls 1989).

Pesticides applied to farm crops can also be carried into adjacent water bodies (Ryder and Johnson 1972). Body burdens of pesticides, mercury, and polychlorinated biphenyls have been documented in lake trout in Lake Simcoe, but effects on lake trout survival (and, therefore, effects at the population level) are unknown (Frank et al. 1978).

Finally, land drainage for agricultural purposes could potentially have impacts on aquatic systems through alteration of stream flows and temperature regimes, and release of silt and nutrients (Ryder and Edwards 1985).

Dams and dykes - These works are of concern to lake trout habitat for a number of reasons. First, they can hinder migrations and block access to spawning sites. For example, Smith (1972) described the demise of river-run lake trout from the Great Lakes, and Grimaldi and Numann (1972) cited a similar blocking of lake trout access to spawning grounds in Lake Constance (Bodensee). Second, changes in lake level and discharge regime can lead to intensification of eutrophication or sedimentation by decreasing the flushing rate (Ryder and Johnson 1972). Drowning or exposure of spawning shoals can increase egg mortality, and warming of lake temperature regimes can lead to decreased lake trout summer habitat (Northcote 1972; Ryder and Johnson 1972).

Fire - Fire on the watershed could potentially influence lake trout through increase in the temperature of inflowing streams and the release of nutrients. Ryder and Johnson (1972) estimated that the incidence of fire-induced eutrophication of oligotrophic lakes in Ontario has increased 5-fold due to the activities of man. A study of the limnological effects of forest fire, using one control and two burned basins in the Experimental Lakes Area of northwestern Ontario, found significant increases in runoff and in losses of nitrogen, phosphorus, and potassium from the burned watersheds

in the year following the burn (Schindler et al. 1980). However, monitoring of these basins has indicated the observed effects were transitory (K. Mills, Department of Fisheries and Oceans (DFO), Winnipeg, Man. R3T 2N6, pers. comm.). Lake trout data from this study remain to be analyzed, but are expected to show minimal effects, if any (K. Mills, DFO, pers. comm.).

In summary, the major impacts of stresses related to watershed modifications are brought about primarily through the additions of silt (roads, logging, agriculture, damming) and nutrients (logging, agriculture, fire). Effects of sedimentation primarily occur at the egg and alevin stage, because of the location of spawning and early rearing habitats in the littoral zone. High sedimentation rates may smother eggs directly (if occurring during the incubation phase), or contribute to egg mortality through increased biological oxygen demand and ammonia (if sediments are organic in origin). Ryder and Edwards (1985) state that the various physical intrusions on the watershed have contributed significantly to overall rates of sedimentation on lake trout spawning grounds in the Great Lakes. However, the relative contribution of any one source or type of activity is difficult to evaluate (Smith 1972).

Nutrient inputs may have impacts on lake trout at various stages of their life history: as eggs on spawning shoals and as juveniles or adults in thermally-stratified waters. Cultural eutrophication has resulted in increased growth of algae on spawning shoals, particularly in Lake Ontario (Ryder and Edwards 1985; Sly 1988), and the substantial and widespread shoreline modifications in the lake basin have undoubtedly contributed to this problem in important ways.

DOMESTIC AND INDUSTRIAL EFFLUENTS

Environmental requirements of lake trout are extremely rigorous for a temperate-region fish (Ryder and Edwards 1985) and this makes the species especially susceptible to anthropogenic stresses. Martin and Olver (1976) demonstrated that lakes which contain lake trout were deeper, clearer, colder, better oxygenated, and had a lower total alkalinity, buffering capacity, and dissolved solids than lakes inhabited by other species.

When cultural eutrophication results in environmental degradation and increased algal production, lake trout habitat can be negatively affected (Ryder and Edwards 1985). Conditions are especially

critical in the summer because thermal stratification at that time of year reduces the available habitat for this cold-water species and, with nutrient loading, results in the reduction and even the complete depletion of hypolimnetic oxygen (Ryder and Johnson 1972). Any quantitative and qualitative reduction in the suitable summer deep-water habitat (Marcus et al. 1984) will potentially affect lake trout production.

If man-made waste is disposed in oligotrophic systems that support lake trout, it has the potential, either directly or indirectly, to alter environmental conditions and to stress the population. Most of the impact of man-made waste on lake trout populations can be categorized as coming from two sources: domestic, which usually originates from municipal sources but can also come from shoreline residences and campgrounds in the form of leachate from nearshore septic systems; and industrial, which is usually more varied and can contain complex organic chemicals (Malins et al. 1984; Hodson 1987).

Domestic Sewage

Depending upon its source, effluents from domestic sewage can reach the water body in several forms: raw untreated; raw chlorinated; primary-, secondary-, or tertiary-treated; or as nutrient-enriched leachate. It is uncommon, with modern methods of sewage treatment and with current regulations on discharge, to find raw domestic effluents from municipal systems dumped directly into natural water bodies, except in the case of an emergency, breakdown, or renovation. The immediacy and extent of the impact of this type of effluent on water quality and on the lake trout population depends upon the quantity and type of discharge. There is a general concern that nutrient loading from domestic sources is an important stressor of lake trout populations in Ontario (Lewis et al. 1990).

Direct impact - Studies conducted by Esvelt et al. (1973) indicate that, following primary treatment, municipal waste water was significantly toxic to fish, regardless of whether the waste was principally domestic or included a substantial industrial contribution. Biological treatment removed an average of 75% of the toxicity, while that removed by lime precipitation was about 40%. Chlorination increased the toxicity of treated municipal waste water, and dechlorination with sodium bisulphite completely removed the chlorine-induced toxicity. Alexander et al. (1977) showed with static bioassays that short-term exposure to untreated and secondary-treated domestic sewage effluent

was not lethal to lake trout at concentrations <100%, and that lake trout were more sensitive than were Arctic char (*Salvelinus alpinus*), but less sensitive than lake whitefish.

The direct effects on fish of the various toxic compounds found in domestic sewage are not well documented, especially when synergistic toxic effects are involved. With the exception of organic hydrocarbons, very little toxicological research has been conducted on lake trout (see review, Hodson 1987). There is some evidence that un-ionized ammonia (>30 $\mu g\ L^{-1}$) has a detrimental effect on growth of salmonids (Haywood 1983; Marshall et al. 1987). Specific guidelines and criteria concerning the toxicity of common water quality parameters are provided by Thurston et al. (1979).

If domestic sludge particulate settles on rubble used by spawning lake trout and creates a sediment oxygen demand that depresses the oxygen below 6 $mg\ L^{-1}$, then embryo development and survival could show adverse effects (Carlson and Siefert 1974). More specifically, Garside (1959) has shown that oxygen levels of 4.5 $mg\ L^{-1}$ or less at temperatures ranging from 2.5 to 10°C caused retarded development, delayed hatching, an extended hatching period, reduction of vitelline circulatory structures, and abnormalities of the head and trunk. If the effluent creates a direct chemical or biological oxygen demand that depresses the oxygen level of lake trout habitat below approximately 20-30% saturation, loss of lake trout populations can occur (Evans et al. 1991).

Indirect nutrient impact - One of the most insidious aspects of the discharge of domestic waste effluent into lake trout lakes is probably the general effect on lake eutrophication. In two southern Ontario lakes, Dillon et al. (1986) found that total phosphorous loading from domestic waste disposal systems (primarily cottages) equalled or exceeded inputs from all other sources. There is evidence which suggests that even minor increases in the nutrient supply can result in a significant loss of lake trout habitat, especially in mid- to late summer when habitat is already restricted by thermal stratification and intolerable surface temperatures (McNamee et al. 1987). Although eutrophication can cause oxygen reductions in midwinter (Evans 1978), these are usually not so critical in deep, oligotrophic systems as are midsummer effects.

Increased nutrient loading of lakes will increase primary production. The best evidence for this comes from whole-lake-fertilization studies in the Experimental Lakes Area of Ontario, where phosphorus inputs were closely correlated with primary productivity (Schindler 1975; Schindler et al.

1978; Fee 1979). The relation between phosphorus inputs and chlorophyll concentration is direct and well documented (Sakamoto 1966; Vollenweider 1968). It has been shown that the time delay in this response can vary among lakes according to flushing rate (Schindler 1975).

Increase in lake productivity, as quantified by chlorophyll-*a* concentration, can have a significant negative impact on hypolimnetic oxygen concentrations. Models are available that correlate either nutrients or chlorophyll, or both, coupled with lake morphometry parameters to real hypolimnetic oxygen depletion (Cornett and Rigler 1979; Charlton 1980; Cornett 1989). Where the supply of nutrients increases the algal biomass settling out in the hypolimnion, there is a decrease in the oxygen concentration because of both a sediment oxygen demand and a demand in the water column from settling seston and fine organic particulate. Lakes with a very small hypolimnion relative to the volume of the photic zones are typically most sensitive to hypolimnetic oxygen depletion.

Lake trout have conservative oxygen and temperature requirements (Evans et al. 1991). Since hypolimnetic oxygen levels are closely correlated with surface water productivity, increased surface water productivity will decrease the quantity and quality of the hypolimnetic water that is suitable lake trout habitat. This can become critical in mid- to late summer when hypolimnetic oxygen reduction has advanced while surface temperatures are high and intolerable; the trout are then restricted to a narrow midwater refugium (Evans 1978). Some predictions have already been made about the impact of increased chlorophyll on available late-summer lake trout habitat (Anonymous 1987), and Ryan and Marshall (unpubl. data) have shown that if the ratio of total spring phosphorous ($\mu g\ L^{-1}$) to mean depth exceeds 1.0, then intolerable summer oxygen-temperature regimes may result.

Increased nutrient loading and associated primary productivity, which create increased biological oxygen demand, appears to be the major pathway through which domestic effluents affect lake trout populations, as there is virtually no documented evidence that large inputs of allochthanous organic material originating from domestic waste leads to significant declines in lake oxygen levels (McNamee et al. 1987).

Industrial Sewage

Industrial sewage can be toxic to fish (Hodson 1987). Sedimentation from industrial waste could also physically clog spawning grounds, and like domestic sewage, some industrial wastes could affect

nutrient loading. The primary impact of industrial pollution, however, is through the addition of trace elements and synthetic compounds, and their effects range from toxicity, bioaccumulation, inorganic turbidity, and sedimentation to the loss of vertebrate food, reproduction, and even immune reaction (Ryder and Edwards 1985). Considerable effort has been spent in quantifying the impact of industrial pollutants on fish (see review, Hodson 1987). For lake trout, special emphasis has been placed on determining the role of industrial toxicants and contaminants on lake trout reproduction, and recruitment as they affect population rehabilitation, especially in the Great Lakes (Mac 1988).

Effluents from mining - Although discharge into lake trout waters of industrial waste such as mine tailings can be easily recognized and documented, the impact and significance, except in the case of sedimentation and physical loss of habitat, are difficult to document and are poorly understood. However, it has been concluded, using the toxic-unit concept, that trace metals exceed safe levels when the trace-metal scores for As, Cd, Cu, Pb, Hg, Se, Ag, and Sn total greater than 1.0; and if one metal contributes more than 0.2 to the sum, it is considered to be a significant source of toxicity (Anonymous 1978; Marshall et al. 1987). Batterman and Cook (1981) found that lake trout exposed to water contaminated with a fine taconite tailing discharge had significantly more amphibole fibres in the kidneys and, to a lesser extent the muscle, than lake trout from an unpolluted area. They noted that the fibres were similar to those in the source of the pollution and concluded that ingestion was probably the primary route of fibre intake. However, the physiological impact of this contamination on the lake trout was not determined. Body burdens of inorganic metals such as mercury and its methyl salts increase with increasing age (Bache et al. 1972), but again the physiological implications are not well known (but see p. 60)

Effluents from pulp and paper processing and wood treatment - The wood-processing industry can affect lake trout habitat by increasing COD and BOD and by sedimentation of the substrate used in spawning. The chemicals associated with wood preservation and the chlorinated phenols used by the pulp-and-paper industry could be detrimental to lake trout. Direct evidence of their effect on lake trout is generally wanting; however, there is now research which indicates that pulp-mill effluent can cause gonadal impairment in some cold-water species (P. Hodson, DFO, Mont-Joli, Quebec G5H 3Z4, pers. comm.).

Effluents from the chemical industry - Attempts to rehabilitate lake trout stocks in the Great Lakes indicate that recruitment failure associated with impaired reproduction, early development, and survival appears to be a problem. Circumstantial evidence indicates that contaminants may be involved, although individually none of those routinely measured appear to be the cause (Mac 1988). A large array of complex organic compounds accumulates in lake trout and is also found in their fry (Mac and Seelye 1981). For example, Hesselberg and Seelye (1982) identified 167 anthropogenic organic compounds in lake trout from Lake Michigan. Compared with other species, lake trout, which are keystone predators, show very much higher bioaccumulations of such compounds as DDE, TDE, DDT, Dieldrin, PCBs, and mercury (Armstrong and Lutz 1977; Frank et al. 1978). As with the inorganics, concentrations of PCBs in lake trout also increase significantly with age (Bache et al. 1972). Similarly, the biological effects of these accumulated chemicals might be expected to increase with increasing age, especially if they affect reproductive function.

Early studies on lake trout indicated that DDT concentrations above 10 $\mu g\ g^{-1}$ in adult fish affect reproductive success, causing significant sac-fry mortality (Burdick et al. 1964). As a guideline, it had been suggested that if PCBs exceed 2.5 $\mu g\ g^{-1}$ of adult, then egg mortality would result (Anonymous 1978). However, some later studies did not show a correlation between development and survival of eggs and fry of lake trout and DDT and PCB concentrations (Stauffer 1979; Mac et al. 1981).

Some contaminants have been shown to elicit rather subtle responses in lake trout fry. Lake trout fry exposed to PCBs and DDE preferred significantly lower water temperatures (9.6°C as compared with 11.2°C) (Mac and Bergstedt 1981), and fry exposed to these chemicals had impaired swimming ability (Rottiers and Bergstedt 1981). Berlin et al. (1981) have shown from long-term rearing that fry exposed to PCB and DDE have a mortality rate twice as high as that of the controls. Original research suggested that the water contained deleterious agents, because it was shown that eggs from Lake Michigan lake trout did not hatch as well in Lake Michigan water as they did in well water (Stauffer 1979; Edsall and Mac 1982). From more recent research, however, it has been concluded that high lake trout fry mortality is not related to the rearing water but to factors, possibly contaminants, associated with the eggs and sperm (Mac et al. 1985). Maternally inherited contaminants appear to have the potential for the greatest impact (Mac 1988). Indeed, Mac et al. (n.d.) have shown that the hatch of lake trout eggs was correlated with certain PCB congeners (chemical species within the PCB group) they contained and that mortality occurred during the final stages of yolk-sac absorption and swim-up ("swim-up mortality syndrome").

More precise techniques now exist to study the effects of these synthetic organic compounds on fish. Luxon et al. (1987) from field sampling studies have demonstrated the utility of measuring mixed-function oxidase activity of lake trout for monitoring biologically meaningful levels of polyaromatic hydrocarbons and chlorinated hydrocarbons in contaminated environments. They demonstrated that hepatic aryl hydrocarbon hydroxylase activity of lake trout was correlated with PCB levels.

Other effluents - Through biomagnification, lake trout, which are primarily piscivorous and slow-growing, would be expected to show higher levels of contaminants than most other fish species. Radioactivity has been measured in lake trout, although at very low levels (Armstrong and Lutz 1977). The biological significance of this and of the other trace elements and compounds that are present is unknown.

Thermal effluents probably would not affect lake trout directly unless conditions were very extreme or occurred when the fish were entrapped. Like most species, lake trout are quite resistant to short-term exposure to relatively high temperature. Adults regularly make foraging forays into the epilimnion in the summer when temperatures reach 22°C (J. Casselman, pers. comm.). Also, lake trout fry can tolerate temperatures up to 23.5°C (Gibson and Fry 1954). It seems more likely that thermal effluent would affect lake trout in a more subtle fashion by decreasing the amount of thermally suitable summer habitat that is available.

LONG RANGE TRANSPORT OF POLLUTANTS

Many chemicals are emitted into the atmosphere, transported long distances, and eventually reach land and water through wet and dry deposition. Transported substances that are toxic and/or bioaccumulate in fish are discussed, and their effects on lake trout populations are examined. Emphasis is placed on pollutants for which extensive chemical data are available. Many substances (for example, As, DDT, Zn, PCB, toxaphene) are not included here, because of a lack of extensive data on lake water chemistry, body burdens in fish, or atmospheric deposition. The potential effects of long range transport of acidic deposition, mercury (Hg), cadmium (Cd), copper (Cu) and lead (Pb) on lake trout populations are examined.

Acidic Deposition

Concerns - It has been well established that long range transport of acidic deposition results in the loss of fish populations (Harvey and Lee 1982). A wet SO_4 loading of >20 kg $ha^{-1}yr^{-1}$ has been reported to cause damage to sensitive aquatic ecosystems (Memorandum of Intent 1983). Beggs et al. (1985) estimated that 55% of the provincial lake trout resource receives loadings of >20 kg ha^{-1} yr^{-1} wet sulphate and is, therefore, in danger of acidification. This estimate presents strong evidence for potential future losses of lake trout populations, if emissions are not reduced. In comparison to Ontario's other major sport fish species, lake trout is the species most at risk, because of the sensitivity of the early life stages and their susceptibility to acidic runoff in the spring.

Toxicity - The principal mechanism of fish population loss in acidified systems is successive recruitment failure (mortality of early life stages) (Beggs and Gunn 1986). No evidence has been found for effects of long range transport on adult lake trout. Field surveys of acidified lakes (pH <5.5), with remnant lake trout populations, show that the adult lake trout continue to spawn, produce viable eggs and sperm, and show good growth rates and condition factors (Beggs and Gunn 1986). They documented lake trout recruitment failures in the following low pH lakes in Ontario: Florence (pH 4.8); Lumsden (pH 4.9); Jerry (pH 4.9); Bowland (pH 5.0); Laundric (pH 5.2); George (pH 5.3); and Michaud (pH 5.6).

Netting surveys of 36 native lake trout lakes in Ontario showed that populations fail to recruit at pH <5.5 (Beggs and Gunn 1986). Verification for this pH threshold was found in Whitepine Lake near Sudbury (Beggs and Gunn 1986). Prior to 1980, the lake trout population consisted of large, old fish (>15 yr, lake pH <5.5). Reductions in sulphur emissions resulted in improved water quality in Whitepine Lake (pH 5.63, 1982), and successful lake trout recruitment. A similar lake trout threshold (pH 5.6) was found in the experimental acidification of Lake 223 (Mills et al. 1987). Failure of ion-regulation appears to be the primary toxic response of fish to low pH (Wood and McDonald 1982). Dissolved organic carbon (DOC) and total Al concentration have also been shown to be important components of the acidification problem (Beggs and Gunn 1986). Acidification causes mobilization of aluminum from soils and rock into lakes (Driscoll et al. 1980). Aluminum is toxic to fish and its concentration in lakes was found to be correlated with extinction of lake trout in Ontario (Beggs et al. 1985). The toxicity of Al is dependent on pH and the presence of organic ligands (DOC). Toxicity increases as pH declines, but Al complexes with organic ligands which

decreases its toxicity. Toxicity of Al in natural waters is variable, therefore, depending on pH and DOC.

Extent of the problem - To date, of the 2196 extant lake trout lakes in the province, 1296 (55.9%) have been sampled for lake water chemistry. To estimate the provincial lake trout resource currently affected by acidic deposition, the number of lakes with pH <5.5 (threshold for recruitment failure) was estimated. Estimates were based on extrapolations from the sampled population to the total provincial resource, by watershed. Given the high percentage of the total resource that has been sampled and the homogeneity of water chemistry within a watershed, these data probably present accurate estimates of resources at risk.

An estimated 4.1% of Ontario lake trout lakes have a pH <5.5 (threshold for recruitment failure). Based on lake water chemistry, we would predict that the populations in these lakes would show signs of recruitment failure. Most of these lakes (74%) are located in the Sudbury area (defined as the area bounded by latitudes 4600-4730'N and longitude 8000-8130'W). This area historically received high loadings of SO_4 deposition from local smelting operations (Beggs et al. 1985).

The same methods were used to estimate the percent of the provincial lake trout resource with alkalinity <40 μeq L^{-1}. Lakes with alkalinities below this concentration would be classified as being extremely sensitive to acidic deposition, having little or no buffering capacity to neutralize damaging acidic deposition. An estimated 15.4% of the provincial lake trout resource has alkalinities of less than 40 μeq L^{-1}, and would be classified as extremely sensitive to acid loadings. The majority of these lakes are located in Algonquin and Northeastern regions. These regions receive SO_4 deposition levels potentially damaging to sensitive aquatic resources (> = 20 kg $ha^{-1}yr^{-1}$; Tang et al. 1986a, b).

A relatively small percentage of Ontario's lake trout resource is currently affected by acidic deposition. However, a high proportion of the lake trout resource has low alkalinity (<40 μeq L^{-1}) and receives potentially damaging acid loadings (>20 kg $ha^{-1}yr^{-1}$). Acidification may have a large impact on the provinces lake trout resource in the future, if emissions are not reduced.

Mercury Deposition

Concern - Mercury (Hg) is emitted into the atmosphere from two major sources, fossil fuel combustion and manufacturing processes (Reed et al. 1979). The OMOE has recently initiated a program to measure long range transport of Hg, through its deposition monitoring network. Currently, no data are available to determine deposition patterns, although Johnson (1987) found Hg in lake sediments to be widespread, but apparently not primarily atmospheric in origin.

A guideline of 0.1 $\mu g\ L^{-1}$ total mercury in water has been set to protect aquatic organisms and to ensure that fish are acceptable for human consumption (Reed et al. 1979). With the exception of lakes affected by point sources, Hg levels are generally below detection levels in inland lakes in Ontario. Reservoirs provide a notable exception in which Hg concentrations can be elevated (Jones et al. 1986). Concentrations of Hg in uncontaminated water range from 0.001-0.01 $\mu g\ L^{-1}$ (Richmond et al. 1988). Despite the low levels in lake water, Hg levels in fish flesh exceed the human health criteria level (<0.5 mg kg^{-1} in fish flesh) in many lakes distant from any local human source of Hg contamination. Hg in fish flesh, however, is positively correlated with loadings to lake sediments (Johnson 1987). Approximately 20% of the 2,905 lake trout sampled in inland lakes (data from the *Guide to Eating Ontario Sport Fish*, OMOE and OMNR 1988) exceed the human health concentration. Of the 191 lake trout lakes sampled, 67% contained fish that exceed the human health criteria. The data from the *Guide to Eating Ontario Sport Fish* are provided to illustrate the extent of the problem, and should not be interpreted further without accounting for differences in fish length and age between lakes.

These data should be interpreted with caution. When Hg concentrations in fish from different lakes are compared, it is essential to take into account the length of exposure to the contaminant (age of the fish). There is a strong relationship between Hg concentration in lake trout and fish length (McMurtry et al. 1989). Fish length is often used to represent exposure time when age data are not available.

Mercury in reservoirs - Mercury has been found to accumulate in fish to unacceptably high levels following impoundment of reservoirs, even in the absence of anthropogenic sources of Hg. This pattern has been reported from reservoirs in the United States and Canada (Jones et al. 1986). A literature review and laboratory experiments reported by Jones et al. (1986) failed to provide a

basis for a generally applicable model of this phenomenon. However, high Hg concentration in reservoirs was proposed to be a function of a number of factors, which may vary temporally and geographically. These factors are reservoir location, water hardness, extent of flooding (and the nature of the flooded areas), erosion potential, and the fish species present. None of these factors is consistently dominant. There is strong evidence that Hg levels change as a reservoir ages, with a general pattern of early increase followed by later declines, but the timing of the pattern is variable. Soil and vegetation in the flooded area appear to comprise the source of the Hg.

The impacts on Hg in fish flesh can be significant. In reservoirs constructed on the La Grande River in Quebec, Hg levels in piscivore flesh exceeded the federal consumption guideline of 0.5 mg kg^{-1}. The data for lake trout are very limited. Most of the reservoirs represented in the review by Jones et al. (1986) contained cool-water species; only four of the 31 reservoirs in their data base contained lake trout, and for each of these, there was only 1 yr of data.

Toxicity - There is no evidence in the field that Hg causes mortality or sublethal effects in fish. Mortality has been observed in the laboratory, however, concentrations tested exceed those found in the field. An average 96 h LC_{50} of 75 $\mu g\ L^{-1}$ was obtained using yearling and juvenile brook trout (McKim et al. 1976). A maximum acceptable toxicant concentration for young brook trout was between 0.93 $\mu g\ L^{-1}$ (some effect) and 0.29 $\mu g\ L^{-1}$ (no effect). Mortality or sublethal effects have not been observed for walleye in the English-Wabigoon River system, which represents the worst documented situation in Ontario, where an estimated 9,000-23,000 kg methyl-mercury was released into the river system between 1962-1970. Fish from Clay Lake, on the Wabigoon River system, contained Hg concentrations of 10-20 mg kg^{-1} in fish flesh, the highest levels ever reported for freshwater fish (Parks et al. 1984). In the English-Wabigoon River area, human health effects have been reported; however, no effects have been documented for the fish population (N. Ward, OMNR, Kenora, Ont. P9N 3X9, pers. comm.).

Work conducted by Swedish researchers (Lindahl and Schwanbom 1971) indicated an effect on the central nervous system in fish with low levels of Hg in the fish muscle. Swimming ability was impaired in fish with Hg concentrations of 0.232 mg kg^{-1} in muscle. Forty-five percent of the lake trout sampled in the *Guide to Eating Ontario Sport Fish* (OMOE and OMNR 1988) had body burdens of Hg exceeding this concentration. Hg concentrations in lake trout in 90% of sampled lakes exceed this Hg concentration.

Factors influencing Hg concentrations in lake trout - Mercury concentrations in fish have been reported to be elevated in low pH systems (Wren and MacCrimmon 1983; Suns et al. 1987). However, the exact mechanism to account for the effects of lake pH on Hg levels in fish is unknown.

The relationship between Hg in lake trout of a standard length (44 cm) and 20 lake physical/chemical parameters was examined for 91 lake trout lakes across Ontario (McMurtry et al. 1989). Of the physical-chemical variables examined, only dissolved organic carbon explained a significant amount (37%, $P < 0.05$) of the variation in Hg concentrations in lake trout. Predator-prey relationships might also influence the bioaccumulation of Hg (see p. 35).

Results from a questionnaire included in the 1986 *Guide to Eating Ontario Sport Fish* (OMOE and OMNR 1988) showed that fishing effort and exploitation rate may be reduced in lakes reported to have high body burdens of contaminants. Fifty-three percent of the respondents indicated that their fish consuming and/or fishing habits had changed as a result of the published information. Of these respondents, 10% returned larger fish back to the lake and 9% changed their fishing location.

Mercury concentrations are elevated in many lake trout lakes in Ontario remote from direct human sources of Hg. Johnson (1987) found that Hg loadings to lake sediment from precipitation was 1- to 3-times background loadings from edaphic sources. Little data are available to suggest that concentrations in Ontario are toxic to fish, but this aspect has not been studied in detail. Laboratory studies on the long-term effects of Hg on fish are needed. Comprehensive field studies are also needed to determine processes by which Hg becomes elevated in fish.

Lead Deposition

Concerns - The major sources of lead (Pb) in the environment are: coal burning, automobiles using leaded fuel, cement manufacturing, and waste incineration (Demayo et al. 1980). Lead is transported through the atmosphere, however, it clears fairly quickly and concentrations decrease as distance from source increases. OMOE deposition data showed that Pb deposition follows a north-south gradient with highest deposition in southern Ontario (>6.0 mg m^{-2} (Tang et al. 1986a, b). In 14 Ontario lakes, Pb concentration in sediments was greater than all other trace metals, being 900% of background levels (pre-1900) on average (Johnson 1987). Johnson (1987) concluded that Pb loadings were mostly anthropogenic and atmospheric in origin.

Toxicity - The distribution of Pb through the ecosystem indicates that it does not bio-concentrate in the aquatic food web (Demayo et al. 1980). Long-term effects of exposure to Pb were studied over three generations of brook trout (Holcombe et al. 1976). The maximum acceptable toxicant concentrations for brook trout in soft water were found to be between 58.0-119.0 $\mu g\ L^{-1}$ total Pb (Holcombe et al. 1976). Lead toxicity is related to fish age with the early life stages most affected. This is thought to be related to either the high sensitivity of the developing embryo's nervous system or to increased uptake of Pb by very young fish (Hodson et al. 1979). Lead causes developmental deformities, such as spinal curvatures, reduced growth, blackening of the tail, and excess mucus production which interferes with respiratory exchange (Hodson et al. 1979).

Lead toxicity in fish is a function of alkalinity; tolerance for Pb increasing with increasing alkalinity (OMOE 1981). For protection of aquatic organisms, the OMOE has recommended that concentrations not exceed the following:

Alk. mg L^{-1}	Max. Pb $\mu g\ L^{-1}$ (OMOE 1981)
<20	5.0
20-40	10.0
40-80	20.0
>80	25.0

Extent of the problem - Extensive lake chemical data were analyzed, to determine the extent of lakes with Pb concentrations exceeding the water quality guidelines (OMOE 1981). Of the 590 lakes sampled, only those in the Sudbury area are known to contain lake trout. The preliminary data suggested that Pb concentrations in Ontario lakes are generally well below the OMOE criteria for protection of aquatic organisms. With restrictions on leaded gasoline, Pb concentrations in the environment should not increase. Therefore, atmospheric sources of Pb in lake water does not appear to be a serious threat to Ontario's lake trout populations. Little is known, however, about the effects of accumulated Pb in lake sediments, or about its mobility into the food web. Based on concentrations of Pb in lake sediments and fish, Johnson (1987) concluded that Pb has a relatively low potential for net uptake by fish compared to eight other trace elements including, in order of relative uptake, Hg, zinc, selenium, copper, cadmium, arsenic, nickel, and chromium.

Copper Deposition

Concern - The major sources of copper (Cu) in Canada are manufacturing (smelting), pig iron production, and wood and coal burning (Demayo and Taylor 1981). High Cu loadings are found in southern Ontario, near major industrial sources (annual wet deposition 2.33 mg m^{-2} of Cu), and in the Sudbury area (1.4-1.3 mg m^{-2} of Cu) (Tang et al. 1986a, b). Deposition decreases with distance from major sources (Tang et al. 1986a, b). Copper emissions in the Sudbury area were historically very high. Emission reductions have resulted in improved air quality in the Sudbury area (Keller and Pitblado 1986). Many of the Sudbury area lakes, however, currently have very high Cu concentrations, due to historically high Cu loadings (Keller and Pitblado 1986).

Toxicity - Uptake of Cu by fish occurs at the gill surface (Anderson and Spear 1980). In general, small fish have a larger lamellar surface area on the gills, compared to larger fish, therefore, more sites for Cu uptake per unit body weight and higher Cu concentrations. Generally, the concentration of Cu in muscle decreased as the size of the fish increased (Anderson and Spear 1980).

The sublethal and lethal effects of Cu on fish are: reproductive failure; mortality of eggs and fry; changes in osmoregulation; respiration effects; cessation of feeding; changes in blood parameters; and growth reduction (Demayo and Taylor 1981). The maximum acceptable toxicant concentration was found to be between 9.5 and 17.4 $\mu g\ L^{-1}$ for brook trout in soft water (McKim and Benoit 1971). The permissible level of Cu in water thought to be safe for aquatic life is <5.0 mg $L\ 1^{-1}$ (OMOE 1981).

Extent of the problem - Extensive lake chemical data were examined from three regions to determine the extent of lakes with Cu concentrations exceeding the OMOE guideline. The sampled Sudbury area lakes all contain (or historically contained) lake trout. Fish species data were not collected as part of the Northwestern Region and Algonquin Region surveys and, therefore, these lakes may or may not contain lake trout. These chemical data should, therefore, be used only to determine the extent of Ontario's lakes with high Cu concentrations.

Region	Wet dep** Cu mg m^{-2}	No. lakes sampled for Cu	No. [Cu] >5.0 $\mu g\ L^{-1}$
Northwestern Region	<1.1	300	20
Sudbury	1.47	200*	11
Algonquin	1.5-1.3	20	0

*All lake trout lakes.
**Data from Tang et al. (1986a, b).

Copper concentrations exceed OMOE guidelines in 6.6% of the sampled lakes in Northwestern Region and 5.5% of the Sudbury area lakes. These data should be interpreted with caution. First, Cu concentrations appear to be extremely variable in many of the lakes with mean concentrations >5.0 $\mu g\ L^{-1}$. For example, in one lake sampled for Cu 7-times over a 4 yr period, concentrations ranged from 1.0-10.6 mg L^{-1}, with a median of 3.0 and a mean of 6.0. These data suggest that Cu has high temporal variation in lakes. Copper has a high affinity for dissolved organic carbon (DOC) which is known to be temporally variable. Secondly, in some lakes with high Cu, other metals are also very high, suggesting inputs from mining or smelting operations. The lakes with high Cu were located in Northwestern Region and the Sudbury area. All lakes sampled in the Algonquin area had low concentrations of Cu. This is probably a function of biases in the data set rather than the true distribution of Cu concentrations across Ontario. The Algonquin area lakes are all OMOE/OMNR research-monitoring lakes. These lakes were chosen because they have no point source inputs. The Northwestern Region and Sudbury area samples are from extensive lake survey programs. Extensive lake Cu data are not available for Algonquin Region lakes.

Cadmium Deposition

Concern - Cadmium (Cd) commonly occurs as greenockite (CdS), which is a by-product of zinc refining. Canada is the world's third largest producer (11.5%) of Cd. The main anthropogenic sources of Cd in the environment are mining, metal smelters, manufacturing (paints, batteries), fertilizers, pesticides, and fossil fuel (Environment Canada 1979).

Annual wet deposition of Cd is highest in southwestern Ontario (124-271 $\mu g\ m^{-2}$ of Cd) and lowest in northwestern Ontario (62-34 $\mu g\ m^{-2}$ of Cd) (Tang et al. 1986a, b). No evidence can be found for higher Cd concentrations in predators compared to their prey, therefore, Cd does not bioaccumulate in the food web (Reed et al. 1979).

Toxicity - Cadmium is extremely toxic to aquatic organisms (OMOE 1981). The toxicity of Cd is greater in soft water than in hard water. The OMOE has set a Cd concentration of <0.2 $\mu g\ L^{-1}$ for protection of aquatic life (OMOE 1981). The maximum acceptable toxicant concentration of Cd for lake trout was found to be between 4.4 and 12.4 $\mu g\ L^{-1}$ for lake trout held for 60 d in soft water (Eaton et al. 1978).

Extent of the problem - Very few chemical data are available on Cd concentrations in water in Ontario's lakes. The only data available were from six lakes in Algonquin Region, and all lakes have concentrations below 0.2 $\mu g\ L^{-1}$, the OMOE threshold for protection of aquatic life. Johnson (1987) reported Cd levels in sediments of 14 lakes from across Ontario, and found that concentrations in the sediments were correlated with concentrations in fish.

The potential effects of Cd on aquatic organisms could pose a very serious environmental problem. Cadmium has widespread use in fertilizers and pesticides throughout southern Ontario. All Ontario lakes receive loadings of Cd through atmospheric deposition (Tang et al. 1986a, b). Until concentrations in lake water and fish tissues are assessed on an extensive basis, no conclusions can be made on the effects of Cd on lake trout populations.

DISCUSSION

Assessment of the health of lake trout populations requires the acquisition of field data and the use of standard criteria for diagnosis of the state of the fish production system. It is appropriate that assessment be focused at the population level, although where diagnosis requires identification of causal relationships, observations will almost certainly be required at other levels of the ecosystem. The influence of habitat variables (Marcus et al. 1984) and other species (Evans et al. 1987; Goddard et al. 1987) on the dynamics of lake trout populations, clearly indicates the need for an ecosystem approach (Ryder and Edwards 1985).

Rapport et al. (1981, 1985) suggested that the general adaptation syndrome (GAS) of Selye (1973), which characterizes the suite of non-specific responses of the vertebrate body to external stimuli, has a counterpart in ecosystem response. Rapport et al. (1985) cited successional changes that follow forest fires in temperate regions, and the transformation from dominance of large to small

species caused by excessive harvesting of benthic fish populations in temperate lakes as examples characterized by predictable, generalized ecological responses analogous to the stress responses of humans and other vertebrates. Rapport et al. (1981) argued that understanding of the general patterns of ecological response underlying these processes will contribute to our ability to utilize, protect and rehabilitate natural systems. Accordingly, they proposed that the medical approach to diagnosis of disease be used to facilitate development of a more critical approach to the diagnosis, treatment and rehabilitation of degraded ecosystems. Their ecosystem distress syndrome (Rapport et al. 1981), which identifies such criteria as change in body sizes of organisms in a community, reduced species diversity, shortened food chain length, and reduced stability of populations, however, is primarily a retrospective approach to assessing the health of aquatic communities. Often, the damage has long since been done and information, collected during a population collapse, is later used to piece together the course of past events. The ecosystem distress syndrome, however, provides a well documented model of the ecological consequences of anthropogenic stressors. As we now know, ecosystem degradation, once engaged, is not easily reversed (Francis et al. 1979; Steedman and Regier 1987), nor is restoration of lost lake trout stocks (Eshenroder et al. 1984). Ecosystem management, including fisheries, requires an anticipatory assessment approach incorporating monitoring, diagnostic tools, and effective regulatory mechanisms. In the case of lake trout, this will require quite specific knowledge about population response mechanisms and modes of actions of particular stressors, clearly incorporated within an integrated, holistic model of lake trout production systems.

LAKE TROUT RESPONSE-TO-STRESS SYNDROME

In the absence of exploitation and other disturbances, lake trout populations are dominated by large, long-lived individuals (Johnson 1972, 1976, 1980; Healey 1978b; Power 1978). Unexploited lake trout population structures have only been studied in Arctic lakes, because elsewhere, undisturbed populations are exceedingly rare. We suggest that similar population structures would probably have been found in lower latitude lakes as well, prior to disturbance by humans, notwithstanding the effects of temperature on natural mortality rates and longevity (Beverton and Holt 1959; Pauly 1980), which would tend to shorten life spans at lower latitudes.

In unexploited lake trout populations, we expect to find a slowing down of growth with increasing body sizes and an accumulation of fish in the larger size categories as more fish grow into a given length interval than grow out of it in the same time period (Johnson 1981). Populations of large bodied, long-lived fishes, such as lake trout, respond in predictable ways to stressors that cause mortality of their individuals. Angling for example will tend to remove the larger fish, large individuals being highly vulnerable to capture (Healey 1978b). Thus, age structures of highly exploited stocks will be less positively skewed than moderately exploited or unexploited ones simply as a result of having relatively fewer old fish, as was demonstrated in simulation studies by Evans et al. (1991), and is clearly seen by comparing Arctic stocks versus stocks near the southern bounds of the lake trout's range. If mortality of the adults is sufficiently extreme, none will reach maturity, reproduction will be eliminated, and extinction will be imminent. The only way that lake trout stocks can be maintained in this state is by artificial recruitment (i.e. stocking). If, on the other hand, adult mortality was reduced at this stage of senescence (a shift towards a more youthful structure), in the absence of other stressors, the residual population would soon reestablish reproduction.

The effect of reducing or eliminating recruitment of new year-classes also has predictable consequences for population structure. When mortality operates selectively on the eggs, alevins or fry (e.g. Gunn and Keller 1981; Gunn and Noakes 1987), the number of young fish will decline, while older juveniles and adults would experience normal rates of mortality. The result would be missing year-classes following imposition of the stress, and an increase in mean age and body size of the population as it ages and approaches senescence (a shift towards lower production, reduced fertility, elevated incidence of disease, and higher mortality). If such situations persist for periods exceeding the reproductive life span of the species, local extinction will occur (e.g. Gunn 1982).

Patterns of Population Response to Stress

Juvenescence and senescence are two primary consequences of stress-induced, selective mortality and/or impairment of lake trout populations. These processes reach full expression under the imposition of severe stress, but operate to a lesser degree under normal circumstances as populations fluctuate in abundance under the influence of environmentally or demographically modulated recruitment and mortality schedules. Populations exist in only three basic states: increasing; decreasing; or stable states. We have attempted to describe these population states in terms of population response, generic types of environmental and stressor induced perturbations, changes in population density, mortality patterns, and recruitment variation (Table 7).

TABLE 7. Possible patterns of population status and response of lake trout stocks in temperate lakes. Relative risk of extinction is a function of population size ($T = 2^K$) where T is time to extinction and K is population size (Goodman 1987). Intrinsic rate of increase (higher under juvenescence) and longevity (lower under juvenescence) also influence the risk of extinction (Pimm et al. 1988). A stationary population will potentially vary in non-random ways within some natural domain of stability (Holling 1985) and will incorporate transient characteristics of enjuvenation and senescence as it increases and declines.

Population status	Response mode	Cause	Density (no ha^{-1})	Mortality	Recruitment	Relative risk of extinction
Increasing	Expansive	New habitat; high nutrient subsidy; climate change; reduced stress	High	Status quo Decreased	Increased Status quo	Low
	Juvenescent	Loss of adults; press or pulse perturbations	Increase	Increased for adults, lower for YOY and juveniles	Compensatory increase	Moderate to high
Decreasing	Suppressive	Limiting habitat or degradation of habitat; press perturbations	Decrease	Increased	Decreased	High
	Senescent	Loss of juveniles; pulse or press perturbations	Low	Increased for YOY and juveniles; stable for adults	Declining or lost	High
Stationary	Constant mean, usually with temporally correlated deviations, operating within a natural "domain of stability"	Recruitment variation due to environmental variability, demographic factors, and/or recruitment variation of associated species	Low to high	Low to moderate, stable for all ages	Varies from low to high	Varies from low to high as a function of population size

Populations that are increasing exist in two modes: (1) an expansion mode in which new habitat becomes available, a nutrient subsidy occurs, or a favourable climate change enhances recruitment and decreases mortality rates; and (2) a juvenescent mode in which compensatory recruitment results in increased density of smaller, younger individuals, following a decline in adult density. Juvenescence will, of course, only allow an increase in density up to a point, beyond which the population will rapidly decline, if adult mortality persists (Evans et al. 1991). Juvenescence will occur under the influence of pulse or press type perturbations (Bender et al. 1984) that cause increased adult mortality, especially of large, old fish.

Decreasing populations also exist in two basic modes: (1) a suppressive mode characterized by increased mortality rates at all life stages and reduced recruitment; and (2) a senescent mode in which juvenile mortality increases and recruitment declines. Suppression occurs under the influence of a variety of press-type stressors (Bender et al. 1984) including, for example, limiting or degraded habitat, chronic chemical toxicity, and invasion by exotic species. Senescence occurs in response to pulse- and press-type stressors that cause selective mortality of early life stages, resulting in declining or lost recruitment. If the duration of pulse or press-type stressors exceeds the reproductive life span, extinction occurs.

Stationary (stable) populations undergo increases and decreases revealing the initial stages of juvenescence and senescence in response, to natural environmental and demographic factors. They generally possess enough resistance and resilience (Pimm 1984), however, either to minimize change from some mean density or to return to equilibrium relatively quickly following a major increase or decrease. The density (abundance) of stable populations will vary from low to high, and their recruitment from low to moderate, depending on the availability of suitable habitats, production of the system and the amount of stress experienced by the adult stock.

The risk of extinction varies dramatically, depending on the status and response mode of a population, because risk of extinction is dependent on population size, the longevity of the species, and the intrinsic rate of increase. For lake trout, **increasing and high-density stable populations with broad size and age distributions will have the lowest risk of extinction**. Juvenescent populations under stress will have moderate to high risks of extinction, because of a compressed age structure and the risk of exceeding the capacity for compensatory recruitment. Suppressed and senescent populations will have a high risk of extinction, because of low abundance and reduced potential for increase as a result of lost fitness due to chronic stress and ageing. Stable populations at low density also have a relatively high risk of extinction, due to demographic accidents (Pimm et al. 1988) or chance environmental events.

The extreme responses leading to extinctions, while effective in characterizing patterns of population response (Table 7), are less common and less significant as practical indicators of stress than are the relatively subtle changes in mortality and recruitment rates. In general, stressors reduce the scope for activity of fishes which increases the risk of mortality and results in decreased fitness

(Priede 1977, 1985). Changes in mortality rates, therefore, signal the influences of stressors (both natural and anthropogenic) operating on a population and potential changes in age structure and population status. All populations undergo natural, transient increases and decreases as they respond to the influences of their environments. Separating the transient increases and decreases of populations from the more persistent effects of anthropogenic stressors is a fundamental concern for fisheries managers.

INDICATORS OF STRESS

The possible responses of fish populations to stressors are relatively few and can be divided into first order and second order responses. First order responses are the most important for assessment in our view, because they include readily observable changes in patterns of abundance that occur directly as a result of changes in mortality rates. Second order indicators are changes that occur either as a result of shifts in abundance that influence compensatory population mechanisms, such as changes in growth rates and maturation schedules, or as a result of sublethal effects of stressors that also affect growth rates and reproductive functions.

First Order Indicators

First order responses are those involving changes in abundance of various life history components of the population, as a result of differential mortality effects. The pattern of change in population age and size structure will be indicative of the type of differential mortality that has occurred. An ageing or senescent population that is declining in abundance indicates elevated mortality of the early life stages or reproductive impairment of the adults. A juvenescent population dominated by young fish usually indicates elevated and selective mortality of adults. A suppressed population subjected to both types of mortality will show symptoms of both low recruitment and loss of older individuals, indicating chronic lethal and sublethal effects. The **population age structure and abundance, therefore, provide the first clues concerning the health of a population. Indicators of abundance include catch-per-unit-effort (CUE) or harvest-per-unit-effort (HUE)** obtained from creel or fisheries assessment surveys. Interpretation of this type of information is best accomplished using a comparative approach in which regional geographic factors that might affect productivity are taken into account (Lester et al. 1991). Evans et al. (1991) provided standard curves relating harvest and fishing effort so that harvest from an individual lake can be compared to a larger provincial lake set.

Additional information about size and age structure and maturity, in addition to CUE or HUE, will enable an initial evaluation to be made of the status of a lake trout population and assessment of the relative levels of juvenile versus adult mortality. Actual estimates of mortality and recruitment rates provide further insight into the population dynamics underlying changes in age structure.

Variation in abundance has also been identified as a potentially useful indicator of stress (OMNR 1983; Colby 1984), although the mechanism by which variation arises due to stress is not well understood. The simulation model of Evans et al. (1991) revealed increased cyclical variation in abundance with the imposition of changes in either adult or YOY mortality rates. These changes in recruitment variation appeared to be due to over- and under-compensation of the stock recruitment function entrained by year-class effects, as sudden mortality changes were introduced. Similar overshoots and undershoots might also be characteristic of natural populations, although recruitment variation, due to stochastic environmental and possibly community factors, would tend to mask the cyclical variation caused by year-class effects. Analysis of the 50 yr time series of lake trout abundance in Lake Opeongo (D.O. Evans, OMNR, unpubl. data), using partial autocorrelation analysis (e.g. Evans and Waring 1987), revealed a significant internal partial autocorrelation at a periodicity of 8 yr. Partial autocorrelation, with a periodicity of about one generation time, indicates a density-dependent population mechanism. The square of the partial autocorrelation coefficient is equal to the amount of variation that is transferred from one generation to the next (Garsd 1984).

Second Order Indicators

Second order effects include density-dependent variables that change in predictable ways with changes in abundance. These include growth rate, fecundity and age of maturity. These parameters of fish populations which, in part, comprise the compensatory, density-dependent mechanisms of fishes (Ricker 1975; McFadden 1977; Jensen 1985), have previously been reviewed in the context of response to stressors by Healey (1978a, b), Colby (1984), OMNR (1983), and Munkittrick and Dixon (1989). Healey (1978a) concluded that lake trout growth increases with exploitation, presumably as a function of reduced intraspecific competition for food and, or territory. Healey (1978a) also concluded that insufficient evidence is available to determine unequivocally whether or not size-specific fecundity increases with exploitation, although experimental exploitation of four lakes in the Northwest Territories appears to have caused relative fecundity to increase (Healey 1978a). If growth rate increases with exploitation, and fecundity is a simple function of body size, increased fecundity

at age would be expected. The minimum age of maturity for lake trout appears to be 5-6 yr (Healey 1978b; Martin and Olver 1980). The observed age of first maturity, however, varied from 5-19 yr among 14 populations, suggesting considerable scope for adjustments in maturity schedules (Healey 1978b), although most of the late maturing populations reviewed by these authors were unexploited Arctic stocks and the effect of latitudinal factors on maturity were impossible to factor out.

Direct evidence of enhanced growth rate, fecundity and reduced age of maturity under high exploitation is provided by Power and Gregoire (1978) for lakes in the Ungava Peninsula of Quebec. Lake trout in a lake inhabited by freshwater harbour seals (*Phoca vitulina*) had a much higher growth rate, higher relative fecundity, and matured at less than 9 yr of age compared to lake trout populations in nearby lakes without seal populations, that matured at ages from 10-20 yr. The authors concluded that exploitation by seals brought about the compensatory changes in the maturation schedule of the trout population.

In summary, there is a limited set of possible responses of fish populations to stressors. Colby (1984) has attempted to characterize these into five general response groups (GRPs) with reference to freshwater fishes in general. His scheme attempts to incorporate an understanding of the mechanisms underlying the responses by including several second order factors, such as condition factor and sex ratio. As a routine assessment approach, we suggest that this degree of detailed analysis might not be necessary. As a research approach to provide the knowledge base for interpretation of assessment data, however, it is essential that the fundamental response mechanisms be understood. Our intention is to outline a more generic approach to the problem of diagnosis of stress effects on lake trout populations. **There are only a limited number of possible responses to stress and by using selective field data, basic life history information and relatively simple computer models** (e.g. Evans et al. 1991), **it should be possible to achieve acceptable levels of diagnostic resolution for management.**

Lake Trout Population Status and Response Under Stress

Lake trout populations under stress respond with changes in either birth or death rates, or both. Birth and death rates in stable, unstressed populations, in contrast, are in approximate equilibrium with net reproductive rates fluctuating around one (Jensen 1985). We identified three population modes that correspond to various stress states (Table 7). These are juvenescent, senescent, and

suppressive states, corresponding to increased adult death rate, decreased birth or recruitment rate, and the combined effect of increased death rate and decreased birth rate, respectively. Juvenescent and senescent states are transitional states that potentially lead to new equilibria or to extinction under the influence of press-type stressors. These states are also reversible, however, when pulse-type stressors are released. An example of the latter type apparently occurred in Whitepine Lake, Ontario, an acidified lake in which lake trout reproduction was eliminated for several years, but was subsequently restored as pH returned to tolerable levels after acid deposition was reduced (Beggs et al. 1985). Suppressed populations are generally the result of chronic elevated mortality or sublethal effects that operate on young or adult life stages, or both. The critical factors in the response of lake trout to stress that distinguish the responses and their possible causes are:

- whether mortality affects the early life, or adult stages, or both;
- whether the response is acute or chronic; and
- whether the mortality effects are direct or indirect (sublethal).

All of the stress responses of lake trout and other fish populations, therefore, are ultimately the result of changes in birth and mortality rates, the latter occurring at various life stages, being either acute or chronic and either direct or indirect, depending on the stressor that is involved. Responses of lake trout to various types of stressors are summarized for adults, embryos and alevins, and YOY and juveniles in Tables 8, 9 and 10, respectively. Lethal effects are summarized separately from sublethal or indirect effects. Sublethal effects often, but not always, lead indirectly to mortalities due to latent or delayed effects (Gunn and Noakes 1987; Hodson 1987). Other indirect effects include reduced production, due to chronic impairment of the scope for growth (Munkittrick and Dixon 1988), and competitive interactions and food web effects involving other species (Warner and Fenderson 1963).

The major differences in response to various stressors depend on whether the stressor acts acutely or chronically, and whether the effects occur before or after maturity. The only distinctions in population responses to stressors that can be readily distinguished are whether the response is juvenescent, senescent or suppressive. Juvenescence is caused only by differential, elevated mortality of adults, and primarily occurs as a result of fishing (Table 8). Senescence is caused by differential, acute and chronic mortality of early life stages and can be caused by numerous stressors (Table 9 and 10). A suppressive response is caused by chronic mortality or sublethal effects of press-type stressors

TABLE 8. Effects of potential stressors operating on adult lake trout. Evidence of effects is definitive in some cases, but only circumstantial in others.

Action of stressors	Potential stressors	Possible responses	Possible consequences	Indicators	Population response mode	Evidence in adult lake trout	Evidence in other fish species
Lethal effects	Fishing	• High mortality of the adult brood stock	• Fewer adult fish • Compensatory recruitment • Compensatory capacity exceeded • No recruitment • Vulnerable to extinction	• Increase in adult mortality • Increase in adult growth rate • Initial increase in recruitment • Decline in CUE in weight • Altered size distribution • Decline in mean age and size	Juvenescent Suppressive	Healey (1978a, b) Hoyle and Stewart (1987) Kelther (1972) Power and Gregoire (1978) Clark and Huang (1985)	Regier and Loftus (1972) Numann (1972) Christie (1972)
	Nutrient loading (reduced summer habitat due to O_2 depletion)	• Summer kill	• Reduced abundance • Vulnerable to extinction	• Decline in CUE • Altered age and size structure • Declining growth even at reduced densities	Suppressive	No direct evidence of dead adults	Larkin and Northcote (1969) Casselman and Harvey (1975) Verduin (1964) Coutant (1985) Price et al. (1985)
	Contaminants and toxicants	• Acute mortality • Chronic mortality	• Reduced abundance • Reduced longevity • Extinction	• Increase in mortality rate • Decline in CUE • Altered age structure	Suppressive	None	Ryder and Edwards (1985) Tarrazona et al. (1987) Hodson (1987) Enwik et al. (1973)
Sublethal and indirect effects	Nutrient loading (reduced summer habitat)	• Reduced scope for activity • Increased competition due to crowding	• Reduced feeding • Reduced growth	• Decline in growth rate • Change in age of maturity • Decline in mean body size	Suppressive	Evans et al. (1991) Numann (1972)	Evans (1978) Coutant (1985) Weithman and Haas (1984) Price et al. (1985)

TABLE 6. Continued

Action of stressors	Potential stressors	Possible responses	Possible consequences	Indicators	Population response mode	Evidence in adult lake trout	Evidence in other fish species
Sublethal and indirect effects	Contaminants and toxicants	• Reduced scope for activity • Abnormal gonadal development or maturation schedules • Physiological effects	• Reduced growth • Reduced fertility • Reduced longevity	• Reduced recruitment • Fewer young fish • Change in age and size distribution • Decline in CUE	Suppressive	Burdick et al. (1964) Loftus et al. (1987)	Hodson (1987) Munkittrick and Dixon (1988) Haywood (1983)
	Silt loading	• Spatial displacement • Food web effects • Feeding	• Reduced feeding success • Reduced growth • Reduced body condition	• Reduced production • Reduced recruitment • Decline in CUE	Suppressive	None	Bruton (1985) Crouse et al. (1981) Sigler et al. (1984)
	Spawning habitat degradation or loss (aggregate removal, in-filling, construction, water level fluctuation)	• Displacement from natal spawning sites • Crowding at remaining sites	• Reduced spawning success • Reduced reproductive success	• Reduced recruitment • Fewer young fish • Increase in mean age-body size • Reduced CUE	Senescent Suppressive	Eschmeyer et al. (1964) Sly and Widmer (1984) Youngs and Oglesby (1972) Dorr et al. (1981) Wagner (1981)	Wilber (1983) Benton (1965)
	Species introduction (excludes exotic stocks and species)	• Displacement from natal spawning habitat • Competition for food	• Reduced spawning • Introgressive hybridization • Change in growth rate, depending on whether competitor or prey was introduced • Possible increase in body burden of contaminants • Changes in vulnerability to angling mortality	• Reduced recruitment • Reduced CUE • Change in mean age and body size • Change in maturation schedule	Suppressive Expansive	Goddard et al. (1987) Hennigar and Chaw (1984) MacLean et al. (1981) Martin (1970) McCrimmon and Mullen (1968)	Evans and Loftus (1987) Evans and Waring (1987) Fraser (1978) Colby et al. (1987)

Table 9. Effects of potential stressors operating on lake trout embryos and alevins. Evidence of effects is definitive in some cases, but only circumstantial in others.

Action of stressors	Potential stressors	Possible responses	Possible consequences	Indicators	Population response mode	Evidence on lake trout	Evidence on other fish species
Lethal effects	Nutrient loading - high NH_3 and low dissolved O_2 in rearing sub-stocks	• Complete or partial mortality of embryos	• No recruitment • Partial recruitment • Fewer young fish - reduced recruitment • Extinction	• Fewer young fish • Decline in CUE • Increase in mean age and size	Suppressive Senescent	Sly (1986, 1988) Carlson and Siefert (1974)	Thurston et al. (1978, 1981) Haywood (1983) Rosenbaugh (1988)
	Silt loading - physical smothering of eggs and alevins	• As above	• As above	• As above	Senescent Suppressive	Sly and Widmer (1984) Sly (1994) Hindley (1984)	Bruton (1985) EIFAC (1965) Reiser and Bjornn (1979) Fudge and Bodaly (1984)
	Toxicants	• As above	• As above	• As above	Senescent Suppressive	Eaton et al. (1978) Mac et al. (1985)	Eaton et al. (1973) Alexander et al. (1977) Mount and Dawson (1980) van Winkoop-Hagen (1988)
	Water level fluctuations	• As above	• As above	• As above	Senescent Suppressive	Martin (1955) DeMarche (1969) Wilton (1985)	
	Acidification	• As above	• As above	• As above	Senescent Suppressive	Mills et al. (1987) Beggs and Gunn (1986) Gunn and Keller (1984)	Harvey (1982)

Table 2.9 Continued.

Action of stressor	Potential stressors	Possible responses	Possible consequences	Indicators	Population response mode	Evidence in lake trout	Evidence in other fish species
	Contaminants	• As above	• As above	• As above	Increases Suppresses	Mac et al. (1981) Stauffer (1979) Burdick et al. (1964)	von Westernhagen (1988)
	Introductions	• Increased predation mortality	• Reduced recruitment	• Decline in abundance of young fish • Decline in CUE • Increase in mean age and size	Suppresses	Marcin and Fry (1977) Rhyne and Magnuson (1981) Hennigar and Claar (1984) Stauffer and Wagner (1979)	Loftus and Hudstrom (1988) Chereie (1972)
Substrate effects	Nutrients - (NH_3, low o_2)	• Deformity of embryos and alevins	• Reduced survival of eggs and alevins • Reduced growth	• Fewer young fish • Decreased abundance of adults • Altered age and size distribution • Increase in mean • Increase in mean age • Decline in CUE	Suppresses	Garside (1959) Carlson and Siefert (1974)	Burkhalter and Kaya (1977) Colt and Armstrong (1981) Rosenkough (1988)
	Silt loading	• Behavioural avoidance - displacement from preferred habitats • Reduced feeding of alevins	• Reduced survival of eggs and alevins	• As above	Suppresses	Mussey and Edsall (1989) Sly and Widmer (1984)	Ruttler (1972) Bruton (1985) Englert et al. (1982)

TABLE 9 Continued

Action of stressors	Potential stressors	Possible responses	Possible consequences	Indicators	Population response mode	Evidence in lake trout	Evidence in other fish species
	Acidification	• As above	• Reduced growth • Reduced survival of eggs and alevins; delayed mortality	• As above	Suppressive	Gunn and Keller (1984) Gunn et al. (1987) Gunn and Noakes (1987)	Fromm (1980)
	Toxicants	• Deformity • Reduced growth	• As above	• As above	Suppressive	Stauffer (1979)	von Westernhagen (1988)
	Contaminants	• As above	• As above	• As above	Suppressive	Mac et al. (1981) Mac (1988) Berlin et al. (1981)	Niimi and Cho (1983) Munkittrick and Dixon (1988)
	Introductions	• Competition for space and food	• Reduced growth • Reduced survival	• As above	Suppressive		

TABLE 10. Effects of potential stressors operating on young-of-year and juvenile lake trout. Evidence of effects is definitive in some cases, but only circumstantial in others.

Action of stressors	Two trial stressors	Possible responses	Possible consequences	Indicators	Population response mode	Evidence in lake trout	Evidence in other fish species
Lethal effects	Nutrient loading (NH_3, low O_2)	• Elevated juvenile mortality • Complete or partial mortality	• Reduced survival • Reduced recruitment • Extinction	• Fewer young fish • Altered age structure • Decline in CUE	Suppressive Senescent	No direct evidence of dead YOY	Ayles et al. (1976) Rosenberg (1980) Haywood (1983)
	Contaminants and toxicants	• As above	• As above	• As above	Suppressive Senescent	Berlin et al. (1981)	Webb and Brett (1973) Webster (1975) Mortens and Servizi (1974)
	Introductions (including stocking)	• Predation mortality	• As above	• As above	Suppressive Senescent	Evans et al. (1991) Hassinger and Close (1984)	Zaret and Paine (1973) Christie (1972)
Sublethal effects	Nutrient loading (hypolimnetic dissolved O_2)	• Initial increase in growth • Later growth declines • Spatial displacement • Elevated predation mortality	• Initially, fast growing juveniles become vulnerable to fishing mortality • Reduced recruitment	• Increased growth of adults • Fewer young fish • Altered age-size structure • Decline in CUE	Suppressive	Evans et al. (1991)	Price et al. (1985)
	Contaminants and toxicants	• Reduced scope for activity • Reduced growth	• Elevated chronic mortality of juveniles • Increased vulnerability to predation	• As above	Suppressive	Berlin et al. (1981)	Alexander et al. (1977)
	Introductions	• Impaired growth and activity • Space and food competition • Food web effects	• Increased vulnerability to predation • Elevated mortality	• As above	Senescent	Warner and Fenderson (1963) Hassinger and Close (1984)	Evans and Loftus (1987) Evans and Waring (1987) Crowder et al. (1987)

operating at one or more life stages. Changes in abundance at age, and in mean body size and age are the primary indicators of population change, but as seen in Tables 8-10, these responses are expected under the influence of many stressors. Indeed, these indicators vary over time, even for stable populations, in response to natural environmental variation, although long-lived species such as lake trout have life history strategies adapted for stability in variable environments (Evans et al. 1987). **Major changes in lake trout population structure, therefore, signal the probable presence of a persistent stressor**, simply because the species is well adapted to persist in the face of short-term adversity. Attributing changes to particular stressors, however, is more difficult because of the common response patterns.

The most effective indicators of stress responses are the first order or abundance indicators such as CUE, HUE, age structure, and size structure. Changes in second order indicators (growth rate, age of maturity, fecundity) are much more variable and, therefore, more difficult to detect and attribute to causal factors. Second order indicators, as a result, are of less value in diagnosing stress in lake trout stocks. In a comparative context, however, improved understanding of growth parameters and maturation schedules would be valuable for evaluation of production processes and variation among lake trout lakes. Development of methods for predicting potential production has important implications for evaluating stress effects and for rehabilitation.

DIAGNOSIS OF STRESS IN LAKE TROUT POPULATIONS

Diagnosis of stress in a lake trout population requires a multifaceted approach exemplified by the epidemiological approach outlined by Gilbertson (1984) and Ryder and Edwards (1985). The approach requires certain basic knowledge about the state of the system that can be acquired by well established field procedures, such as lake and fishery creel surveys and short-cut methods of fisheries assessment (Fenchel 1974; Pauly 1980; Hoenig et al. 1987). Questions that need to be addressed are:

- What is the relative abundance of the population in question;
- How does the abundance compare to that expected;
- Has there been any change in abundance;
- What is the population size and age structure;
- What is the mortality rate of the population;
- Is there any recruitment into the population; and

- If there is no recruitment, are there any adult fish of reproductive age in the population.

If these questions can be answered, even in a general way, initial conclusions can be drawn about the state of the population and the possible stressors that might be affecting it. When population changes have occurred, the next step in the process is to evaluate the possible stressors that might be causing the types of effects that are present. At this point, an assessment of the potential stressors should be undertaken to identify which of the possible factors is involved in the population changes. Once the possible candidate stressors have been identified, more specific questions can be addressed to establish causal linkages between the stressor or stressors and the malaise of the population. Tables 8, 9, and 10 provide initial guidelines for linking population responses to the actions of various stressors.

Unifying Themes

Efforts of ecologists to diagnose stress effects on fish populations have tended to concentrate on the diversity and complexity of both the stressors and the responses (OMNR 1983; Colby 1984) with less attention given to providing a unifying diagnostic approach. Rapport et al. (1985) discuss the failure of ecologists to develop the unifying syntheses needed to provide a coherent approach to the problem of protecting and rehabilitating ecosystems. The recent synthesis of Ryder and Edwards (1985) and the dichotomous key which uses the lake trout as an indicator organism for the diagnosis of ecosystem health in the Great Lakes (Marshall et al. 1987; Edwards et al. 1990) are attempts to provide such a synthesis. The dichotomous key addresses the issues of abiotic and biotic environmental influences and the stress effects of exploitation, habitat loss, nutrient loading, pH changes and chemical contaminants specifically in Lake Superior, but a recent update allows evaluation of inland lakes as well (T.R. Marshall, OMNR, Thunder Bay, Ont. P7B 5E7, pers. comm.). The dichotomous key approach provides a listing of the types of questions needed to be addressed in establishing the nature of stressors that might underlie the decline or loss of a lake trout population.

The following check list of potential diagnostics is suggested as a baseline for initial evaluation of stress effects on inland lake trout stocks. We have suggested the general content of the evaluation rather than the specific questions, because these will vary from case to case. Exploitation guidelines and nursery habitat criteria provided herein and in OMNR (1982), Marcus et al. (1984), Ryder and Edwards (1985), Marshall et al. (1987), Evans et al. (1991), and other sources cited in our review

provide specific questions and parameter guidelines for population, habitat, community, and toxicant criteria. The diagnostics check list encompasses four broad areas as follows:

- Lake trout population information: e.g. stock status (wild, self-sustaining versus stocked), population structure and reproductive potential, mortality rates, growth rates, and maturation schedules (see also Payne et al. 1990);
- Fish community information: e.g. structure of the community including relative abundance of key prey, predators and competitors, introduced species, lake trout stocking information (see also Casl et al. 1990);
- Physical and chemical environmental information: habitat concerns including destruction or loss of spawning habitat, water level variation, nutrient inputs, and primary production, temperature and oxygen regimes, seasonal surface water pH, toxicants, and lake trout body burdens of contaminants (see also MacLean et al. 1990); and
- Exploitation information: fishing intensity, seasonal pattern of use, catch and harvest statistics (Evans et al. 1991).

While this list appears extensive and to demand costly data acquisition, it is important to realize that the information does not necessarily need to be highly quantitative for purposes of developing a working diagnosis. Information of this kind is available for many lakes in existing OMNR data bases. Lake matching, in which similar lakes are compared using standard limnological and yield information (Evans et al. 1991), should provide adequate information on expected production and safe fishing intensities for lakes where historical creel survey data are not available. In most cases, however, some data collection, even if from existing data bases, will probably be required to provide an initial assessment of the present status of the system. A checklist of stressors, their sources and relative importance in Ontario lakes is provided in Table 11, to identify the major potential stressors to be considered in any given case.

Interpretation of Diagnostic Information

Similar population responses can be caused by different stressors. For example, any factor that causes mortality of eggs, alevins, or YOY will have similar effects on the abundance and structure of a lake trout population (Table 9 and 10). It is clear that direct evidence of effects will often not be attainable and, therefore, that a deductive process will be required to determine the probable causal relationships. Quantitative models will be essential, if convincing demonstrations of the

TABLE 1[1]. A check list of stressors, their sources, relative importance, and the life stages of lake trout primarily affected. Based on existing theory and empirical evidence, stressors are rated in terms of their detrimental impact on lake trout as follows: high (+ + +), moderate (+ +), and local (+). Stressors for which strong evidence of cause and effect is available are indicated in bold type. Stressors for which information is unavailable are indicated by (?).

Stressor	Primary sources	Perceived and/or potential importance	Life stages directly affected
Exploitation	Angling	+ + +	Adults
	Commercial fishing	+	
	Subsistence fishing	+ (?)	
	Illegal fishing	+ (?)	
Nutrient loading	Municipal sewage	+ + +	Embryos
	Industrial effluents	+	Alevins
	Cottages/lodges	+ + +	Young-of-the-year
	Camp grounds	+ + +	Juveniles
	Agriculture	+ +	Adults
	Forestry	+	
	Atmospheric	+	
Habitat destruction (littoral zone)	Cottage development	+ +	Embryos
	Recreational development (e.g. marinas)	+ +	Alevins
	Waste disposal	+	Young-of-the-year
	Aggregate removal	+	Adult spawners
Silt loading	Agriculture	+ +	Embryos
	Logging	+	Alevins
	Roads	+ +	Young-of-the-year
	Other construction	+ +	
Water level fluctuations	Hydrological structures	+ +	Embryos
			Alevins
Acidification	Atmospheric	+ + +	Embryos
			Alevins
Toxicants and contaminants	Industrial effluents	+ + +	Embryos
	Sewage effluents	+ +	Alevins
	Land fills	+ (?)	Young-of-the-year
	Atmospheric	+	Juveniles
	Agriculture	+ +	Adults
	Forestry practices	+	
Introduced exotic species and diseases	Intentional introductions	+ + +	Embryos
	Natural colonization	+	Alevins
			Young-of-the-year
			Juveniles
			Adults
Introduction of native species and competitors	Unknown	+ + +	Embryos
	Illegal introductions	+ (?)	Alevins
	Unintentional introductions		Young-of-the-year
			Juveniles
			Adults

probable effects are to be achieved (e.g. Evans et al. 1991). We suggest that adequate understanding is presently available to derive reasonable inferences about the causes of most contemporary cases of lake trout population decline. Although the theory to which we refer is relatively well supported by empirical data as developed in this synthesis and demonstrated by Evans et al. (1991), an urgent need exists however to strengthen these inferences, which presently must be viewed largely as untested hypotheses.

Only in the best documented cases, however, will diagnosis be definitive. Therefore, management must operate under some uncertainty and be strongly adaptive. Adaptive management proceeds on the best available advice, but recognizes that management choices will be subject to modification should the response of the system necessitate alteration of management regulations. Indeed, management decisions should explicitly incorporate hypotheses about how the system is being affected by stressors, and management actions should be designed to test those hypotheses. Testing will require some level of monitoring to detect the system response and to enable adjustments to be made accordingly. **Use of computer simulation is recommended as an essential tool in evaluation of management options and to provide a priori information about the magnitudes and time courses of expected responses.** Options that include actions that become locked in after implementation, such as large fish culture operations, should be considered very carefully and, if possible, should be avoided. **Options that emphasize rehabilitation of natural system productivity and minimize artificial interventions are clearly preferred, because they are more harmonious with the ecological processes and limitations that govern ecosystem behaviour and, therefore, have the lowest uncertainty, hence the lowest risk, and usually the least short- and long-term costs.**

MANAGEMENT IMPLICATIONS

STATUS OF THE LAKE TROUT RESOURCE

The native lake trout resource has been seriously degraded in southern Ontario (Eastern, Central, Algonquin regions) and in the Northern and Northeastern regions, as only 33, 42, and 54% of the stocks in those areas are wild, self-sustaining, unstocked populations. These areas support 62% of the total lake trout resource in Ontario, representing 661 wild self-sustaining stocks. All of the remaining wild stocks (813, 55%) are found in the Northeastern and North Central regions of Ontario. In these two regions, 99 and 89% of the stocks are entirely self-sustaining.

We recommend that emphasis be placed on protection of the remaining self-sustaining wild stocks. Analyses by Evans et al. (1991) suggest that at least some stocks have been transformed to put-grow-and-take hatchery stocks, as a consequence of the combined effects of high exploitation rates and stocking. A more detailed inventory of stocks is needed to establish the degree of genetic transformation that has occurred. This will be a function of the number of years and intensity of stocking and applies primarily to the introduction of non-native stocks. **A moratorium on stocking of non-native stocks should be considered for populations that have not been seriously damaged.** Our recommendations are not intended to imply that wild stocks should not be exploited. However, fishing must be managed to protect the genetic diversity of the species as a whole. In many cases, this will necessitate harvest restrictions. Emphasis needs to be placed on sustainability of the natural production systems upon which lake trout depend and also on not exceeding the natural compensatory capacities of these populations. Exploitation of these stocks is possible and obviously beneficial from a human perspective, but excessive exploitation, environmental degradation and habitat loss must be avoided if the resource is to survive and if optimal productive capacity is to be achieved.

MAJOR STRESSORS

The stressors that are most commonly perceived by OMNR field staff to be affecting Ontario lake trout stocks are exploitation, habitat degradation, and species introductions, including stocking of non-native lake trout and the loss of genetic diversity (Lewis et al. 1990). Our review of the major stressors supports these impressions, although the discrepancies between perception and reality noted for acidic precipitation effects by Lewis et al. (1990) might also apply to survey results for other stressors as well. Nevertheless, the reported frequencies and geographic patterns of concern for particular stressors provided a valuable perspective; one that has guided our review and detailed analyses (Evans et al. 1991).

Exploitation

One concern about the effects of fishing on lake trout populations that needs to be reconsidered by managers is the impact of winter angling on total harvest and mortality rates. As early as 1954, Martin (1954) showed that winter anglers removed significantly more small and immature lake trout during winter than during summer. The implications of increasing the mortality rate of pre-adult fish is that recruitment into the reproductive age groups would be very significantly reduced. (Payne et

al. 1990; Evans et al. 1991). This was not recognized in the early 1950s when winter fishing was opened throughout most of Ontario. Removal of lake trout from a population as pre-adults, before they have made a reproductive contribution, may be particularly harmful, if the objective is to manage for self-sustaining stocks (Payne et al. 1990). It would not appear to be simply circumstantial that lake trout lakes in Algonquin Park, that are closed to winter fishing, continue to be self-sustaining, while many nearby lakes that are subjected to winter angling are clearly showing symptoms of excessive exploitation (Hoyle and Stewart 1987; Evans et al. 1991). Exploitation during other seasons could also result in excessive adult mortality rates, although lake trout appear to be less vulnerable during open water seasons, especially to unskilled anglers (Shuter et al. 1987; Evans et al. 1991).

Maintenance of self-sustaining stocks of lake trout will be difficult, if not impossible, unless harvests are restricted to levels that allow adequate escapement and spawning of the adult stock. One way of achieving reductions in harvests would be to restrict or terminate winter fishing. The consequences of not adequately controlling harvests include the potential loss of many local stocks, and increasing expenditures for supplemental stocking of hatchery-reared fish. Other options for restricting harvests are available, but would possibly require increased monitoring and higher administrative expenditures. For example, limited entry fisheries, season catch limits, lake specific catch quotas, seasonal fishing restrictions, gear and bait restrictions, or species catch restrictions are alternative methods for restricting harvests, some of which (seasonal fishing restrictions, bait restrictions, species catch restrictions, i.e. bag, slot, and size limits) are presently in force. **In general, regulations are needed to improve the balance between actual predation of lake trout and fishing harvests to achieve optimal benefits without causing incremental damage to the resource base, including loss of genetic diversity and overall vitality.**

Introductions

With the exception of sea lamprey in the Great Lakes, there is little definitive evidence to indicate that introduced exotic species have had much influence on lake trout populations. Introduction of rainbow smelt, however, appears to have had some significant effects on lake trout stocks. Rainbow smelt apparently exert their effects on lake trout mainly through the food web, although some evidence of predation by smelt on lake trout fry has been documented (Stauffer and Wagner 1979; Hassinger and Close 1984). Increased growth rates and bioaccumulation of mercury in lake trout are two apparent consequences of smelt introductions. The uncertainty and potential risks associated

two apparent consequences of smelt introductions. The uncertainty and potential risks associated with smelt introductions led Evans and Loftus (1987) to conclude that the species should not be introduced into lakes supporting naturally reproducing stocks of cold-water species. Also, in consideration of the tendency of smelt to disperse via down-stream movement and thereby to colonize new habitats, **we strongly recommend that smelt not be introduced into any inland waters.**

Several indigenous species possibly have significant effects on lake trout production in inland lakes in Ontario, including lake whitefish, burbot and walleye (Goddard et al. 1987; Carl et al. 1990). In particular, **we caution against introduction of walleye into small lakes with native lake trout populations.**

Stocking of hatchery-reared lake trout on self-sustaining, but suppressed wild stocks, is a common management practice in Ontario. **We caution that supplemental stocking poses a serious threat to the wild stock, because of the risks of introgressive hybridization and the suppressive effects of artificial recruitment on wild fish.** Evans et al. (1991) have shown that the combined effects of high exploitation and high stocking rates cause serious suppression and ultimate extinction of wild stocks subjected to this practice.

Habitat Modifications

Habitat loss poses a serious threat to wild lake trout populations in Ontario. Loss of spawning and early rearing habitat due to shoreline modifications, substrate extraction, disposal of dredged materials, and water level fluctuations are the most serious nearshore effects. We conclude that reduction in the number or area of spawning and early rearing habitats, or degradation of the quality of these habitats is detrimental to the production of healthy self-sustaining lake trout stocks. There is no evidence to demonstrate that *K*-adapted species such as lake trout can compensate for losses in habitat or impaired early survival. Degraded spawning and early rearing habitats would be expected to result in reduced recruitment and lower production of wild self-sustaining lake trout stocks. **We recommend that protection of sensitive habitats receive the highest management priority.**

Watershed Modifications

The most important influences of watershed effects are silt and nutrient loading to lakes.

Construction of roads and associated developments, logging, agriculture, construction of dams, and forest fire are primary sources of silt and nutrients to lake trout lakes. The importance of these stressors is variable and often primarily of local significance, but cumulative effects province-wide should not be underestimated. Roads and construction projects are common sources of silt loads to inland lakes, perhaps being the most widespread sources. Historically, logging and agriculture have also been very important contributors of silt and nutrients, especially to lakes Ontario and Simcoe in southern Ontario, both of which have lost natural recruitment of lake trout. As a **general conclusion, we caution that lake trout early life habitats are very susceptible to silt and nutrient loading, and that precautions should be taken to prevent substantive increases in the input of these materials.**

Domestic and Industrial Effluents

Domestic sewage and industrial effluents containing toxic chemicals can have a wide spectrum of acute and chronic effects on lake trout, including direct lethality, physiological and reproductive impairment, and reduced longevity (Evans et al. 1988). Numerous indirect effects are also known, including habitat degradation, behavioural avoidance, and effects on abundances of prey species. The most important of the indirect effects of domestic sewage effluents on lake trout lakes is on lake eutrophication. Nutrient loading due to domestic sewage inputs causes increased primary production, increased biological oxygen demand, and consequently depletion of ambient dissolved oxygen concentrations in the hypolimnion during summer. Loss or reduction of water quality in the deep hypolimnion has been shown to be a potentially important constraint in the production of lake trout in Ontario lakes (Evans et al. 1991). Nutrient loading can, in some cases, cause increased production of attached algae in the littoral (*Cladophora* spp.) and sublittoral (*Dichotomosiphon tuberosus*) zones, resulting in alteration of those habitats for lake trout as a result of the annual decomposition of the algae.

Protection of lake trout populations from direct inputs of toxic chemicals into their environment is obviously also a very high priority for management, if wild self-sustaining stocks are to be maintained. We have already noted the importance of protecting lake trout habitat from degradation or loss, and emphasize that domestic and industrial effluents can potentially exert numerous negative influences, although documentation of effects is generally incomplete.

Long-range Transport of Atmospheric Pollutants

Transport of pollutants in the atmosphere is a problem of global proportions, but there is ample evidence of local and regional effects of airborne acid and toxic chemicals on aquatic ecosystems due to Ontario sources. In the case of acidification, the sources and population effects on lake trout populations are well documented, but the effects of toxic chemicals and contaminants on free-ranging fish stocks have not yet been adequately described, even though strong circumstantial evidence is available (Evans et al. 1990). Lethal effects of airborne toxicants have not yet been demonstrated, but based on the published literature it is possible that sublethal effects are occurring in large long-lived species like lake trout. A potentially equally important aspect is the effect of bioaccumulation of chemical contaminants on fish eating species, including humans.

DIAGNOSIS OF STRESS

A major problem faced by field managers in addressing questions of stress effects on natural populations is to establish with some degree of certainty that: 1) non-random changes have occurred in a particular population and, 2) that the changes are in fact due to a particular stressor. To accomplish this, managers require information not only about the fish populations, but also about the status of fish habitats; the extent of natural variation in meteorological and hydrological processes that might have, either directly or indirectly, influenced the natural recruitment of the fish populations; and the presence, nature, intensity, and temporal aspects of human activities and associated ecosystem stressors within the watershed.

The extensive data collection and associated analysis, implied by these information needs, initially appear to be well beyond the capability of the local biologists and managers for a number of reasons. These include high costs of field data collection, staff constraints, lack of availability of scientific expertise and major gaps in existing knowledge. How do we tackle these problems in dealing with fisheries issues at the local level? Our initial response to this question is that there is no simple answer, but that there are solutions. These solutions require detailed work and analysis, involving some data collection in the field and compilation of pertinent existing information as outlined earlier. We recommend a multifaceted approach which incorporates information synthesis and modelling,

The objective for management is to develop a credible analysis, which draws reasonable inferences based on the best available theoretical arguments and supporting data. We have outlined the type of information that is required to document fish population responses to stress and have referenced the supporting published scientific literature. Our conclusion from this is that some types of stress responses can be readily attributed, but fish populations often respond in similar ways even when subjected to quite different stressors. For example, any of a number of stressors that cause acute or chronic mortality of early life stages will result in similar senescent or suppressive population responses. Attributing these effects to causal factors will require knowledge of the stressors operating on the population. In the case of two or more stressors operating simultaneously, it might be impossible to separate the effects without very detailed studies.

The difficulty of attributing causal effects is not simply one of determining whether effects are occurring, because the evidence of effect of many stressors is overwhelming, simply by association. The difficulty is in providing quantitative evidence in the form of field observation and measurement that links the time and place of the fatalities, physiological impairment and lost production of lake trout with the causative factors. Not only is definitive attribution of the causes of population changes often difficult, but reversing the effects of stressors such as nutrient and silt loading, contaminants and toxicants, or introduced species is difficult, if not impossible, even if effects are clearly demonstrated. Ample evidence exists confirming the difficulties of rehabilitating degraded fish populations and their ecosystem (Harris et al. 1982; Eshenroder et al. 1984). This leads to the conclusion that **management should operate in an anticipatory mode to prevent problems before they become established. We recommend adoption of an anticipatory, proactive approach that embraces a perspective which promotes the idea that monitoring of the health of aquatic ecosystems, rather than the diagnosis of pathology, should be the priority activity.** The information requirements are not very different, but the management environment is dramatically different. Decisions evolving from a proactive health-monitoring program would be made from a position of knowledge, established scientific and societal consensus, and certainty rather than from a position of uncertainty, confusion and compromise, which is synonymous with a reactionary diagnostic approach.

Monitoring health presupposes that we know how to recognize a healthy population or ecosystem and that we are prepared and able to set criteria or objectives that must be met. Activities that compromise these objectives (i.e. the health of a lake trout population, for example) would not be

persisted. Objectives or criteria to identify healthy populations and ecosystems are urgently needed to protect the remaining lake trout resource. Alternate or compromise strategies for development would be clearly seen as destructive of the natural ecosystems upon which they impose. The choices then become clear: to destroy or not to destroy, or to destroy some populations or ecosystems and to save others. These are societal choices beyond the scope of this report. The point to be made, however, is that structuring a proactive program comprised of fisheries management and ecosystem objectives, supported by theoretical and quantitative arguments concerning responses of lake trout or other species to anthropogenic stressors, is the desired position from which to evaluate decisions about the use of aquatic resources.

RECOMMENDATIONS

- Sustainability of the aquatic ecosystem should be explicitly recognized as the first priority of fisheries management, because lake trout and other associated aquatic species are totally dependent on the health of their ecosystems for survival and vitality.
- Management should emphasize protection and conservation of environmental quality and the specific habitats and associated biota that are necessary for the survival and self-sustainability of native fish and other key aquatic species.
- Management should safeguard the genetic diversity of natural aquatic ecosystems, including lake trout, and recognize the implications of incremental loss of genetic diversity for the vitality and sustainability of natural lake trout populations and their associated biota by:
  - managing lake trout stocks to protect the genetic diversity of the species and emphasizing conservation of the remaining self-sustaining wild stocks;
  - expanding the genetic inventory of lake trout stocks;
  - conducting rigorous scientific evaluation of the genetic implications of any fish stocking activity prior to approval;
  - ceasing stocking of hatchery-reared lake trout on self-sustaining wild stocks;
  - instituting a moratorium on stocking of non-native stocks, except where native stocks have been lost; and
  - emphasizing alternative approaches other than stocking for rehabilitation of the self-sustaining productive capacities of stressed wild stocks.
- Management should develop means to control all human activities to ensure that the natural

compensatory capacities of natural ecosystems, including fish stocks, are not exceeded, in order to maximize the ecological, social, economic, aesthetic, and human health benefits of stable, naturally self-sustaining aquatic ecosystems. Specific controls for lake trout include:

- control of harvest and restriction of winter fisheries as necessary to prevent overexploitation of the vital stock;
- placing greater emphasis on defining and protecting the sensitive and vital habitats of key species by:
  - preventing inputs of fine sediments and nutrients beyond those that can be safely assimilated, without transformation or degradation of the system;
  - preventing inputs of toxic and/or bioaccumulating chemicals;
  - reduction of long-range transport of atmospheric pollutants; and
  - increasing research efforts to define life histories and vital habitats of key species;
- prohibiting introduction of exotic species such as rainbow smelt into inland lakes; and
- controlling introductions of native species into inland lakes, such as potentially harmful introduction of walleye into small lakes having native stocks of lake trout;

- Management should adopt an anticipatory, proactive mode through the use of effective research, assessment, monitoring, enforcement of regulations, policy development, and education in which the health of aquatic and associated terrestrial ecosystems receives first priority.
- Management should set improved objectives for managing the health of aquatic ecosystems for society and develop methods, criteria and regulatory mechanisms by which these objectives can be measured, regulated, and enforced. The objectives need to establish the highest priority for the health of natural ecosystems, thereby providing for a proactive rather than reactive management system.

ACKNOWLEDGMENTS

We thank C.I. Goddard, and P.J. Colby for their helpful criticism and advise on an earlier draft. We especially thank C.H. Olver for his detailed scientific and technical editing. The section on mercury uptake by lake trout was contributed by Michael J. McMurtry, Lake Simcoe Fisheries Assessment Unit. G.L. Cunningham and T. Chen coordinated, compiled, and analysed the data for the lake trout questionnaire. We thank them for their dedication to this task and their important contribution to this study. Numerous other OMNR staff were contacted during the preparation of

this manuscript. Thanks is expressed to all who contributed information. We also thank Mary Hirst for typing various drafts of the text and tables.

REFERENCES

AKEILASZEK, J. J., AND T. A. HAINES. 1981. Mercury in the muscle tissue of fish from three northern Maine lakes. Bull. Environ. Contam. Toxicol. 27: 201-208.

ALEXANDER, D. G., K. J. SUPEENE, B. C. CHU, AND H. D. MACIOROWSKI. 1977. The lethal and sublethal effects of secondary-treated sewage effluent on various fish and invertebrates. Fish. Mar. Serv. Tech. Rep. 709. vi + 21 p.

ANDERSON, H. W. 1970. Relative contributions of sediment from source areas, and transport processes, p. 55-63. *In* Forest Land Uses and Stream Environment. Continuing Education.

ANDERSON, P. D., AND P. A. SPEAR. 1980. Copper pharmacokinetics in fish gills. 1. Kinetics in pumpkinseed, *Lepomis gibbosus*, of different body sizes. Water Res. 14: 1101-1105.

ANONYMOUS. 1978. Great Lakes water quality agreement of 1978. Int. Joint Comm., Windsor, Ont. 52 p.

ANONYMOUS. 1980. File report 1980-1. Ont. Min. Nat. Resour., Algonquin Fish. Assess. Unit, Whitney. 3 p.

ANONYMOUS. 1987. Inland lake trout management in eastern Ontario. Ont. Min. Environ., Ont. Min. Nat. Resour., draft report. 56 p. + appendices.

ANONYMOUS. 1988. An evaluation of selected lake trout spawning shoals in Lake of Bays. Tarandus Assoc. Ltd., Environ. Consultants, Brampton, Ont. 47 p.

ANTHONY, D. D., AND C. R. JORGENSEN. 1977. Factors in the declining contributions of walleye (*Stizostedion vitreum vitreum*) to the fishery of Lake Nipissing, Ontario, 1960-76. J. Fish. Res. Board Can. 34: 1703-1709.

ARMSTRONG, F. A. J., AND A. LUTZ. 1977. Lake Superior, 1974: PCB, chlorinated insecticides, heavy metals and radioactivity in offshore fish. Can. Fish. Mar. Serv. Tech. Rep. 693. vi + 17 p.

ARMSTRONG, G. C. 1961. Winter sport fishing in Ontario. Ont. Dep. Lands Forests, Fish. Wildl. Rev. 1(3): 2-7.

AUERBACH, S. I. 1981. Ecosystem response to stress: a review of concepts and approaches, p. 29-42. *In* G.W. Barrett and R. Rosenberg [ed.] Stress effects on natural ecosystems. John Wiley & Sons, New York, Toronto. 305 p.

AYLES, G. B., J. G. I. LARK, J. BARICA, AND H. KLING. 1976. Seasonal mortality of rainbow trout (*Salmo gairdneri*) planted in small eutrophic lakes of central Canada. J. Fish. Res. Board Can. 33: 647-655.

BACHE, C. A., J. W. SERUM, W. D. YOUNGS, AND D. J. LISK. 1972. Polychlorinated biphenyl residues: Accumulation in Cayuga Lake trout with age. Science 177: 1191-1192.

BALL, H. 1988. The dynamics of a polyphagous lake trout population in a northwestern Ontario lake, Thunder Bay, Ontario. M.Sc. thesis, Lakehead Univ., Thunder Bay, Ont. 234 p.

BARRETT, G. W., AND R. ROSENBERG. 1981. Stress effects on natural ecosystems. John Wiley & Sons, New York, Toronto. 305 p.

BATTERMAN, A. R., AND P. M. COOK. 1981. Determination of mineral fiber concentrations in fish tissues. Can. J. Fish. Aquat. Sci. 38: 952-959.

BEETON, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Oceanography 10: 240-254.

BEGGS, G. L., AND J. M. GUNN. 1986. Response of lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) to surface water acidification in Ontario. Water Air Soil Pollut. 30: 711-717.

BEGGS, G. L., J. M. GUNN, AND C. H. OLVER. 1985. The sensitivity of Ontario lake trout (*Salvelinus namaycush*) and lake trout lakes to acidification. Ont. Fish. Tech. Rep. Ser. No. 17. 24 p.

BENDER, E. A., T. J. CASE, AND M. E. GILPIN. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65: 1-13.

BERLIN, W. H., R. J. HESSELBERG, AND M. J. MAC. 1981. Growth and mortality of fry of Lake Michigan lake trout during chronic exposure to PCB's and DDE. U.S. Fish Wildl. Serv. Tech. Pap. 105: 11-22.

BEVERTON, R. J. H., AND S. J. HOLT. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics, p. 142-180. *In* G.E.W. Wolstenholme and M. O'Connor [ed.] CIBA foundation colloquia on ageing. Vol. 5. The lifespans of animals. J. & A. Churchill Ltd., London. 324 p.

BOND, W. A. 1974. The Great Slave Lake commercial fishery, summer, 1973. Environ. Can., Fish. Marine Serv. Tech. Rep. Ser. CEN/T-74-8. 38 p.

BOND, W. A., AND T. D. TURNBULL. 1973. Fishery investigations at Great Slave Lake, Northwest Territories 1972. Environ. Can., Fish. Mar. Serv. Tech. Rep. Ser. CEN/-73-7. 77 p.

BORASKI, J. P. 1983. Incubation and emergence studies on Devil Lake, 1982. Ont. Min. Nat. Resour., Rideau Lakes Fish. Assess. Unit Rep. No. 7.

BORMANN, F. H., G. E. LIKENS, T. G. SICCAMA, R. S. PIERCE, AND J. S. EATON. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecol. Monogr. 44: 255-277.

BRUGAM, R. B. 1978. Human disturbance and the historical development of Linsley Pond. Ecology 59: 19-36.

BRUTON, M. N. 1985. The effects of suspensoids on fish. Hydrologia 125: 221-241.

BURDICK, G. E., E. J. HARRIS, H. J. DEAN, T. M. WALKER, J. SKEA, AND D. COLBY. 1964. The accumulation of DDT in lake trout and effect on reproduction. Trans. Am. Fish. Soc. 93: 127-136.

BURKHALTER, D. E., AND C. M. KAYA. 1977. Effects of prolonged exposure to ammonia on fertilized eggs and sac fry of rainbow trout (*Salmo gairdneri*). Trans. Am. Fish. Soc. 106: 470-475.

CAIRNS, V. W., P. W. HODSON, AND J. O. NRIAGU, [ED.]. 1984. Contaminant effects on fisheries. Vol. 16. Environmental science and technology. John Wiley and Sons, New York. 333 p.

CARL, L., M.-F. BERNIER, W. CHRISTIE, L. DEACON, P. HULSMAN, D. LOFTUS, D. MARALDO, T. MARSHALL, AND P. RYAN. 1990. Fish community and environmental effects on lake trout. Lake trout synthesis. Ont. Min. Nat. Resour., Toronto. 47 p.

CARLANDER, K. D. 1969. Handbook of freshwater biology. Iowa State University Press, Ames. 752 p.

CARLSON, A. R., AND R. E. SIEFERT. 1974. Effects of reduced oxygen on the embryo and larva of lake trout (*Salvelinus namaycush*) and largemouth bass (*Micropterus salmoides*). J. Fish. Res. Board Can. 38: 1393-1396.

CASSELMAN, J. M. 1986. Scale, otolith, and growth characteristics of juvenile lake trout: criteria for discriminating between indigenous and hatchery fish from the natural environment. Great Lakes Fish. Comm. Res. Compilation Rep.

CASSELMAN, J. M., AND H. H. HARVEY. 1975. Selective fish mortality resulting from low winter oxygen. Verh. Int. Verein. Limnol. 19: 2418-2429.

CHARLTON, M. N. 1980. Hypolimnion oxygen consumption in lakes; discussion of productivity and morphometry effects. Can. J. Fish. Aquat. Sci. 37: 1531-1539.

CHRISTIE, W. J. 1957. The bass fishery of Lake Opeongo. MA thesis, Dept. Zool., Univ. Toronto, Toronto, Ont. 77 p.

CHRISTIE, W. J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913-929.

CHRISTIE, W. J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827-854.

CHRISTIE, W. J., J. M. FRASER, AND S. J. NEPSZY. 1972. Effects of species introductions on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 969-973.

CLARK, R. D., JR., AND B. HUANG. 1983. The dynamics of competition between sport and commercial fishing: effects on rehabilitation of lake trout in Lake Michigan. Mich. Dep. Nat. Resour. Fish. Div., Fish. Res. Rep. 1909. 62 p.

CLAYTON, R. R., A. MATHERS, AND N. G. MacLEAN. 1984. The winter sport fisheries on Big Clear, Big Rideau, Big Salmon, Charleston and Devil lakes, 1984. Ont. Min. Nat. Resour., Rideau Lakes Fish. Assess. Unit Rep. No. 13. 75 p.

COBERLY, C. E., AND R. M. HORRALL. 1980. Fish spawning grounds in Wisconsin waters of the Great Lakes as identified by 85 commercial fishermen. Draft. University of Wisconsin Marine Studies Centre, Sea Grant Inst., Madison.

COLBY, P. J. 1984. Appraising the status of fisheries: rehabilitation techniques, p. 233-257. *In* V.W. Cairns, P.V. Hodson and J.O. Nriagu [ed.] Contaminant effects on fisheries. John Wiley and Sons, New York. 333 p.

COLBY, P. J., P. A. RYAN, D. H. SCHUPP, AND S. L. SERNS. 1987. Interactions in north-temperature lake fish communities. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 104-128.

COLT, J. E., AND D. A. ARMSTRONG. 1981. Nitrogen toxicity to crustaceans, fish, and molluscs, p. 34-47. *In* L.J. Allen and E.C. Kinney [ed.] Proc. Bio-Engineering Symp. for Fish Culture. Fish. Cult. Sect., Am. Fish. Soc. and Northeast Soc. Conserv. Eng., Bethesda, MD.

CORNETT, R. J. 1989. Predicting changes in hypolimnetic oxygen concentrations with phosphorus retention, temperature, and morphometry. Limnol. Oceanogr. 34: 1359-1366.

CORNETT, R. J., AND F. H. RIGLER. 1979. Hypolimnetic oxygen deficits: their prediction and interpretation. Science 205: 580-581.

COUTANT, C. C. 1985. Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. Trans. Am. Fish. Soc. 114: 31-61.

CROUSE, M. R., C. A. CALLAHAN, AND K. W. MALUEG. 1981. Effects of fine sediments on growth of juvenile coho salmon in laboratory streams. Trans. Am. Fish. Soc. 110: 281-286.

CROWDER, L. B., M. E. McDONALD, AND J. A. RICE. 1987. Understanding recruitment of Lake Michigan fishes: the importance of size-based interactions between fish and zooplankton. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 141-147.

CROWE, W. R. 1975. Great Lakes Fishery Commission history, program and progress. Great Lakes Fish. Comm., Ann Arbor, MI. 22 p.

CURRIER, J. P., AND F. H. SCHULTZ. 1954. The history of Lake Minnewanka with reference to the reaction of lake trout to artificial changes in environment. Can. Fish Cult. 15: 1-9.

DADSWELL, M. J. 1974. Distribution, ecology, and post-glacial dispersal of certain crustaceans and fishes in eastern North America. Nat'l Mus. Nat. Sci. Publ. Zool. No. 11.

DARNELL, R. M. 1976. Impacts of construction activities in wetlands of the United States. U.S. EPA Ecol. Res. Rep. EPA-600/3-76-045. 392 p.

DAVIS, J. C. 1975. Minimum dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. J. Fish. Res. Board Can. 32: 2295-2332.

DEMAYO, A., AND M. C. TAYLOR. 1981. Guidelines for surface water quality. Vol. 1. Inorganic chemical substances, copper. Inland Waters Directorate, Water Quality Branch, Ottawa, Ont.

DEMAYO, A., M. C. TAYLOR, AND S. W. REED. 1980. Guidelines for surface water quality. Inorganic chemical substances, lead. Inland Waters Directorate, Water Quality Branch, Ottawa, Ont.

DEPARTMENT OF PUBLIC WORKS. 1975. Report to the Government of Canada and the United States of America by the International Working Group on the Abatement and Control of Pollution from Dredging Activities. Dep. Public Works, Ottawa, Ont.

DeROCHE, S. E. 1969. Observations on the spawning habits and early life of lake trout. Prog. Fish-Cult. 31: 109-113.

DILLON, P. J., K. H. NICHOLLS, W. A. SCHEIDER, N. D. YAN, AND D. S. JEFFRIES. 1986. Lakeshore capacity study: trophic status. Min. Municipal Affairs, Toronto, Ont. 89 p.

DONALDSON, E. M. 1981. The pituitary-interrenal axis as an indicator of stress in fish, p. 11-47. *In* A.D. Pickering [ed.] Stress and fish. Academic Press, London. 367 p.

DORR, J. A., III, D. V. O'CONNOR, N. R. FOSTER, AND D. J. JUDE. 1981. Substrate conditions and abundance of lake trout eggs in a traditional spawning area in southeastern Lake Michigan. N. Am. J. Fish. Manage. 1: 165-172.

DRISCOLL, C. T., JR., J. P. BAKER, J. J. BISOGNI, JR., AND C. L. SCHOFIELD. 1980. Effects of aluminum speciation on fish in dilute acidified waters. Nature 284: 161-164.

DUCKWORTH, G. A. 1982. Lake Temagami and Cross Lake summer creel census report, 1981, including an assessment of the annual lake trout fishery on Lake Temagami. Ont. Min. Nat. Resour., Temagami Dist. Ms Rep. 90 p.

EATON, J. G., J. M. McKIM, AND G. W. HOLCOMBE. 1978. Metal toxicity to embryos and larvae of seven freshwater fish species. 1. Cadmium. Bull Environ. Contam. Toxicol. 19: 95-103.

EDSALL, C. C., AND M. J. MAC. 1982. Comparative hatching success of lake trout eggs in Lake Michigan water and well water. Prog. Fish Cult. 44: 44-48.

EDWARDS, C. J., R. A. RYDER, AND T. R. MARSHALL. 1990. Using lake trout as a surrogate of ecosystem health for oligotrophic waters of the Great Lakes. Int. Assoc. Great Lakes Res. 16: 591-608.

EMBODY, G. C. 1934. Relation of temperature to the incubation periods of eggs of four species of trout. Trans. Am. Fish. Soc. 64: 281-292.

EMERY, L. 1985. Review of fish species introduced into the Great Lakes, 1819-1974. Great Lakes Fish. Comm. Tech. Rep. 45.

ENGLERT, J. J., W. A. GRANT, AND B. F. BIETZ. 1982. Impact of logging and associated practices on salmonid standing crop in the Maritimes. Environ. Can., Surv. Rep. No. EPS-5-AR-82-4.

ENVIRONMENT CANADA. 1979. Guidelines for surface water quality. Vol. 1. Inorganic chemical substances - mercury. Can. Dep. Environ., Inland Waters Directorate, Water Quality Br., Ottawa, Ont.

ESCHMEYER, P. H. 1954. The reproduction of lake trout in southern Lake Superior. Trans. Am. Fish. Soc. 84: 47-74.

ESHENRODER, R. L., T. P. POE, AND C. H. OLVER. [ED.] 1984. Strategies for rehabilitation of lake trout in the Great Lakes; Proceedings of a conference on lake trout research, August 1983. Great Lakes Fish. Comm. Tech. Rep. 40. 63 p.

ESVELT, L. A., W. J. KAUFMAN, AND R. E. SELLECK. 1973. Toxicity assessment of treated municipal wastewaters. J. Water Pollut. Control Fed. 45: 1558-1572.

EUROPEAN INLAND FISHERIES ADVISORY COMMISSION. 1965. Water quality criteria for European freshwater fish. Report on finely divided solids and inland fisheries. EIFAC Tech. Pap. 1. Air Water Pollut. 9: 151-168.

EVANS, D. O. 1978. An overview of the ecology of the lake whitefish *Coregonus clupeaformis* (Mitchill) in Lake Simcoe, Ontario. Ont. Min. Nat. Resour., Lake Simcoe Fish. Assess. Unit Rep. 1978-1. 132 p.

EVANS, D. O., AND D. H. LOFTUS. 1987. Colonization of inland lakes in the Great Lakes region by rainbow smelt, *Osmerus mordax*: their freshwater niche and effects on indigenous fishes. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 249-266.

EVANS, D. O., AND P. WARING. 1987. Changes in the multispecies, winter angling fishery of Lake Simcoe, Ontario, 1961-83: invasion by rainbow smelt, *Osmerus mordax*, and the role of intra- and interspecific interactions. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 182-197.

EVANS, D. O., J. M. CASSELMAN, AND C. C. WILLOX. 1991. Effects of exploitation, loss of nursery habitat and stocking on the dynamics and productivity of lake trout populations in Ontario lakes. Lake Trout Synthesis, Ont. Min. Nat. Resour., Toronto. (In prep.)

EVANS, D. O., G. J. WARREN, AND V. W. CAIRNS. 1990. Assessment and management of fish community health in the Great Lakes: synthesis and recommendations. Int. Assoc. Great Lakes Res. 16: 639-669.

EVANS, D. O., B. A. HENDERSON, N. J. BAX, T. R. MARSHALL, R. T. OGLESBY, AND W. J. CHRISTIE. 1987. Concepts and methods of community ecology applied to freshwater fisheries management. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 448-470.

FEE, E. J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole lake eutrophication experiments. Limnol. Oceanogr. 24: 401-406.

FENCHEL, T. 1974. Intrinsic rate of natural increase: the relationship with body size. Oecologia (Berl.) 114: 317-326.

FRANCIS, G. R., J. J. MAGNUSON, H. A. REGIER, AND D. R. TALHEIM. 1979. Rehabilitating Great Lakes ecosystems. Great Lakes Fish. Comm. Tech. Rep. 37. 99 p.

FRANK, R., M. VAN HOVE HOLDRINET, R. L. DesJARDINE, AND D. P. DODGE. 1978. Organochlorine and mercury residues in fish from Lake Simcoe, Ontario, 1970-76. Environ. Biol. Fishes 3: 275-285.

FRASER, J. M. 1978. The effect of competition with yellow perch on the survival and growth of planted brook trout, splake, and rainbow trout in a small Ontario lake. Trans. Am. Fish. Soc. 107: 505-517.

FROMM, P. O. 1980. A review of some physiological and toxicological responses of freshwater fish to acid stress. Environ. Biol. Fishes 5: 79-93.

FRY, F. E. J. 1939. A comparative study of lake trout fisheries in Algonquin Park, Ontario. Univ. Toronto Stud. Biol. Ser. No. 46. Publ. Ont. Fish. Res. Lab. 58. 69 p.

FUDGE, R. J. P., AND R. A. BODALY. 1984. Postimpoundment winter sedimentation and survival of lake whitefish (*Coregonus clupeaformis*) eggs in Southern Indian Lake, Manitoba. Can. J. Fish. Aquat. Sci. 41: 701-705.

GABOURY, M. N. 1985. A fisheries survey of the Valley River, Manitoba, with particular reference to walleye (*Stizostedion vitreum*) reproductive success. Man. Dep. Nat. Resour. Fish. Ms Rep. #85-02. 149 p.

GABOURY, M. N., AND J. W. PATALAS. 1984. Influence of water level drawdown on the fish populations of Cross Lake, Manitoba. Can. J. Fish. Aquat. Sci. 41: 118-125.

GARSD, A. 1984. Spurious correlation in ecological modelling. Ecol. Model. 23: 191-201.

GARSIDE, E. T. 1959. Some effects of oxygen in relation to temperature on the development of lake trout embryos. Can. J. Zool. 37: 689-698.

GIBSON, E. S., AND F. E. J. FRY. 1954. The performance of the lake trout *Salvelinus namaycush*, at various levels of temperature and oxygen pressure. Can. J. Zool. 32: 252-260.

GILBERTSON, M. 1984. Need for development of epidemiology for chemically induced diseases in fish in Canada. Can. J. Fish. Aquat. Sci. 41: 1534-1540.

GODDARD, C. I., D. H. LOFTUS, J. A. MacLEAN, C. H. OLVER, AND B. J. SHUTER. 1987. Evaluation of the effects of fish community structure on observed yields of lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 239-248.

GOODMAN, D. 1987. The demography of chance extinctions, p. 11-34. *In* M.E. Soulé [ed.] Viable populations. Cambridge University Press, Cambridge, MA. 189 p.

GOODYEAR, C. S., T. A. EDSALL, D. M. ORMSBY DEMPSEY, G. D. MOSS, AND P. E. POLANSKI. 1982. Atlas of the spawning and nursery areas of the Great Lakes fishes. Vol. 1-14. U.S. Fish. Wildl. Serv., Washington, DC, FWS-OBS-82-52.

GRIMALDI, E., AND W. NUMANN. 1972. The future of salmonid communities in the European subalpine lakes. J. Fish. Res. Board Can. 29: 931-936.

GUNN, J. M. 1982. Acidification of lake trout (*Salvelinus namaycush*) lakes near Sudbury, Ontario, p. 351. *In* T.A. Haines and R.E. Johnson [ed.] Acid rain/fisheries. Proc. Int. symp. acid precipitation and fishery impacts in northeastern North America. Cornell Univ., Ithaca, NY, Aug. 2-5, 1981. Northeast. Div. Am. Fish. Soc., Bethesda, MD. 357 p.

GUNN, J. M. 1987. The role of episodic acidification in the extinction of lake trout (*Salvelinus namaycush*) populations. Ph.D. thesis, Univ. Guelph, Guelph, Ont. 133 p.

GUNN, J. M., AND W. KELLER. 1981. Emergence and survival of lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) from artificial substrates in an acid lake. Ont. Fish. Tech. Rep. Ser. No. 1. 9 p.

GUNN, J. M., AND W. KELLER. 1984. Spawning site water chemistry and lake trout (*Salvelinus namaycush*) sac fry survival during spring snowmelt. Can. J. Fish. Aquat. Sci. 41: 319-329.

GUNN, J. M., AND D. L. G. NOAKES. 1987. Latent effects of pulse exposure to aluminum and low pH on size, ionic composition, and feeding efficiency of lake trout (*Salvelinus namaycush*) alevins. Can. J. Fish. Aquat. Sci. 44: 1418-1424.

GUNN, J. M., D. L. G. NOAKES, AND G. F. WESTLAKE. 1987. Behavioural responses of lake charr (*Salvelinus namaycush*) embryos to simulated acidic runoff conditions. Can. J. Zool. 65: 2786-2792.

HACKER, V. A. 1956. Biology and management of lake trout in Green Lake, Wisconsin. Trans. Am. Fish. Soc. 86: 71-83.

HARRIS, H. J., D. R. TALHELM, J. J. MAGNUSON, AND A. M. FORBES. 1982. Green Bay in the future - a rehabilitative prospectus. Great Lakes Fish. Comm. Tech. Rep. 38.

HARVEY, H. H. 1982. Population responses of fishes in acidified waters, p. 227-242. *In* T.A. Haines and R.E. Johnson [ed.] Acid rain/fisheries. Proc. Int. symp. acid precipitation and fishery impacts in northeastern North America, Cornell Univ., Ithaca, NY, Aug. 2-5, 1981. Northeast. Div. Am. Fish. Soc., Bethesda, MD. 357 p.

HARVEY, H. H., AND C. LEE. 1982. Historical fisheries changes related to surface water pH changes in Canada, p. 45-55. *In* T.A. Haines and R.E. Johnson [ed.] Acid rain/fisheries. Proc. Int. symp. acid precipitation and fishery impacts in northeastern North America, Cornell Univ., Ithaca, NY, Aug. 2-5, 1981. Northeast. Div. Am. Fish. Soc., Bethesda, MD. 357 p.

HASSINGER, R. L., AND T. L. CLOSE. 1984. Interaction of lake trout and rainbow smelt in two northeastern Minnesota lakes. Minn. Dep. Nat. Resour., Div. Fish Wildl., Sect. Fish. Invest. Rep. No. 379: 40 p.

HATCH, R. W. 1984. Population dynamics and species interactions, p. 4-9. *In* R.L. Eshenroder, T.P. Poe and C.H. Olver [ed.] Strategies for rehabilitation of lake trout in the Great Lakes: Proceedings of a conference on lake trout research, August 1983. Great Lakes Fish. Comm. Tech. Rep. No. 40. 63 p.

HAYWOOD, G. P. 1983. Ammonia toxicity in teleost fishes: a review. Can. Tech. Rep. Fish. Aquat. Sci. No. 1177.

HEALEY, M. C. 1978a. Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 35: 945-950.

HEALEY, M. C. 1978b. The dynamics of exploited lake trout populations and implications for management. J. Wildl. Manage. 42: 307-328.

HESSELBERG, R. J., AND J. G. SEELYE. 1982. Identification of organic compounds in Great Lakes fishes by gas chromatography/mass spectrometry: 1977. Admin. Rep. No. 82-1, Great Lakes Fish. Lab., Ann Arbor, MI.

HICKS, F. J. 1986. The Opeongo creel survey, 1985-86. Ont. Min. Nat. Resour., Algonquin Fish. Assess. Unit Ms Rep. 11 p.

HILE, R., P. H. ESCHMEYER, AND G. F. LUNGER. 1951. Decline of the lake trout fishery in Lake Michigan. U.S. Fish. Wildl. Serv. Fish. Bull. No. 52: 77-95.

HINDLEY, B. A . 1984. Lake trout and lake whitefish egg survival in Lake Simcoe. M.Sc. thesis, York Univ., Downsview, Ont. 78 p.

HODSON, P. V. 1987. The effect of toxic chemicals on fish. Water Quality Bull. 12: 95-99, 127.

HODSON, P. V., B. R. BLUNT, D. JENSEN, AND S. MORGAN. 1979. Effect of fish age on predicted and observed chronic toxicity of lead to rainbow trout in Lake Ontario water. J. Great Lakes Res. 5: 84-89.

HOENIG, J. M., D. M. HEISEY, W. D. LAWING, AND D. H. SCHUPP. 1987. An indirect rapid methods approach to assessment. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 324-338.

HOLCOMBE, G. W., D. A. BENOIT, E. N. LEANARD, AND J. M. McKIM. 1976. Long-term lead exposure on three generations of brook trout. J. Fish. Res. Board Can. 33: 1731-1741.

HOLLING, C. S. 1985. Resilience of ecosystems: local surprise and global change, p. 228-269. *In* T.F. Malone and J.G. Roederer [ed.] Proc. ICSU 20th General Assembly. Cambridge University Press, London. 512 p.

HORNS, W. H., AND J. J. MAGNUSON. 1981. Crayfish predation on lake trout eggs in Trout Lake, Wisconsin. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 178: 299-303.

HOYLE, J. A., AND T. J. STEWART. 1987. Lake trout exploitation stress assessment on Drag, Dickie and Twelve Mile lakes. Ont. Min. Nat. Resour., Haliburton-Hastings Fish. Assess. Unit, Bancroft. 50 p.

HYATT, K. D., AND J. D. STOCKNER. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. 42: 320-331.

INTERNATIONAL JOINT COMMISSION. 1978. Great Lakes Water Quality Agreement (Canada and the United States). Int. Joint Comm., Windsor, Ont.

IRWIN, K. 1989. A summary of intensive openwater creel surveys, Bancroft District, 1986-87. Ont. Min. Nat. Resour., Bancroft Dist. Fish. Manage. Ms Rep. 1989-01. 141 p.

JENSEN, A. L. 1985. Relations among net reproductive rate and life history parameters for lake whitefish (*Coregonus clupeaformis*). Can. J. Fish. Aquat. Sci. 42: 164-168.

JOHNSON, F. H. 1961. Walleye egg survival during incubation on several types of bottom in Lake Winnibigoshish, Minnesota, and connecting waters. Trans. Am. Fish. Soc. 90: 312-322.

JOHNSON, L. 1972. Keller Lake: characteristics of a culturally unstressed salmonid community. J. Fish. Res. Board Can. 29: 731-740.

JOHNSON, L. 1975. Distribution of fish species in Great Bear Lake, Northwest Territories, with reference to zooplankton, benthic invertebrates, and environmental conditions. J. Fish. Res. Board Can. 32: 1989-2004.

JOHNSON, L. 1976. Ecology of Arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic charr, *S. alpinus* and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. 33: 2459-2488.

JOHNSON, L. 1980. Arctic charr, p. 15-98. *In* E.K. Balon [ed.] Charrs, salmonid fishes of the genus *Salvelinus*. Dr. W. Junk, The Hague, The Netherlands. 928 p.

JOHNSON, L. 1981. The thermodynamic origin of ecosystems. Can. J. Fish. Aquat. Sci. 38: 571-590.

JOHNSON, M. G. 1987. Trace element loadings to sediments of fourteen Ontario lakes and correlations with concentrations in fish. Can. J. Fish. Aquat. Sci. 44: 3-13.

JOHNSON, M. G., AND K. H. NICHOLLS. 1988. Temporal and spatial trends in metal loads to sediments of Lake Simcoe, Ontario. Water Air Soil Pollut. 39: 337-354.

JOHNSON, M. G., AND K. H. NICHOLLS. 1989. Temporal and spatial variability in sediment and phosphorus loads to Lake Simcoe, Ontario. J. Great Lakes Res. 15: 265-282.

JOHNSON, T. B., AND D. O. EVANS. 1990. Size-dependent winter mortality of young-of-the-year white perch: climate warming and invasion of the Laurentian Great Lakes. Trans. Am. Fish. Soc. 119: 301-313.

JONES, M. L., G. L. CUNNINGHAM, D. R. MARMOREK, P. M. STOKES, C. WREN, AND D. DEGRAAF. 1986. Mercury release in hydroelectric reservoirs. Rep. Can. Electrical Assoc. 156 p.

JORGENSEN, C. R. 1973. A summary of the five year study of the Lake Temagami lake trout fishery. Ont. Min. Nat. Resour., Lake Nipissing-Temagami Fish. Manage. Unit Ms Rep. 179 p.

KELEHER, J. J. 1972. Great Slave Lake: effects of exploitation on the salmonid community. J. Fish. Res. Board Can. 29: 741-753.

KELLER, W., AND J. R. PITBLADO. 1986. Water quality changes in Sudbury area lakes: A comparison of synoptic surveys in 1974-1976 and 1981-1983. Water Air Soil Pollut. 29: 285-296.

KRUEGER, C. C., A. J. GHARRETT, T. R. DEHRING, AND F. W. ALLENDORF. 1981. Genetic aspects of fisheries rehabilitation programs. Can. J. Fish. Aquat. Sci. 38: 1877-1881.

LARKIN, P. A., AND T. G. NORTHCOTE. 1969. Fish as indices of eutrophication, p. 256-273. *In* Eutrophication: causes, consequences, correctives. Nat'l. Acad. Sci., Washington, D.C. 661 p.

LASENBY, D. C., T. G. NORTHCOTE, AND M. FURST. 1986. Theory, practice, and effects of *Mysis relicta* introductions to North American and Scandinavian lakes. Can. J. Fish. Aquat. Sci. 43: 1277-1284.

LATHROP, R. C. 1988. Chloride and sodium trends in the Yahara Lakes. Wisc. Dep. Nat. Resour. Res. Manage. Findings No. 12.

LESTER, N. P., M. M. PETZOLD, W. I. DUNLOP, B. MONROE, S. ORSATTI, T. SCHANER, AND D. WOOD. 1991. Sampling Ontario lake trout stocks: issues and standards. Lake trout synthesis. Ont. Min. Nat. Resour., Toronto. (In prep.)

LEWIS, C., G. L. CUNNINGHAM, AND P. CHEN. 1990. Analysis of questionnaire on stresses acting on lake trout lakes. Ont. Min. Nat. Resour., Lake Trout Synthesis Working Group Rep., Toronto. (In prep.)

LI, H. W., AND P. B. MOYLE. 1981. Ecological analysis of species introductions into aquatic ecosystems. Trans. Am. Fish. Soc. 110: 772-782.

LINDAHL, P. E., AND E. SCHWANBOM. 1971. Rotatory-flow techniques as a means of detecting sublethal poisoning in fish populations. Oikos 22: 354-357.

LOFTUS, A. J., W. W. TAYLOR, AND M. KELLER. 1988. An evaluation of lake trout (*Salvelinus namaycush*) hooking mortality in the upper Great Lakes. Can. J. Fish. Aquat. Sci. 45: 1473-1479.

LOFTUS, D. H., AND P. F. HULSMAN. 1986. Predation on larval lake whitefish (*Coregonus clupeaformis*) and lake herring (*C. artedii*) by adult rainbow smelt (*O. mordax*). Can. J. Fish. Aquat. Sci. 43: 812-818.

LOFTUS, K. H., AND H. A. REGIER. Editors. 1972. Proceedings of the symposium on salmonid communities in oligotrophic lakes (SCOL). J. Fish. Res. Board Can. 29: 613-986.

LUGO, A. E., AND J. F. McCORMICK. 1981. Influence of environmental stressors upon energy flow in a natural terrestrial ecosystem, p. 79-102. *In* G.W. Barrett and R. Rosenberg [ed.] Stress effects on natural ecosystems. Chapter 8. John Wiley and Sons, New York, Toronto. 305 p.

LULL, H. W., AND W. E. SOPPER. 1969. Hydrologic effects from urbanization of forested watersheds in the northeast. USDA Forest Serv. Res. Pap. No. NE-146. 31 p.

LUXON, P. L., P. V. HODSON, AND W. BORGMANN. 1987. Hepatic aryl hydrocarbon hydroxylase activity of lake trout (*Salvelinus namaycush*) as an indicator of organic pollution. Environ. Toxicol. Chem. 6: 649-657.

MAC, M. J. 1988. Toxic substances and survival of Lake Michigan salmonids: field and laboratory approaches, p. 389-401. *In* M.S. Evans [ed.] Toxic contaminants and ecosystem health; a Great Lakes focus. John Wiley, New York. 602 p.

MAC, M. J., AND R. A. BERGSTEDT. 1981. Temperature selection by young lake trout after chronic exposure to PCB's and DDE. U.S. Fish Wildl. Serv. Tech. Pap. 105: 33-35.

MAC, M. J., AND J. G. SEELYE. 1981. Patterns of PCB accumulation by fry of lake trout. Bull. Environ. Toxicol. 27: 368-375.

MAC, M. J., W. H. BERLIN, AND D. V. ROTTIERS. 1981. Comparative hatchability of lake trout eggs differing in contaminant burden and incubation conditions. U.S. Fish Wildl. Serv. Tech. Pap. 105: 8-10.

MAC, M. J., C. C. EDSALL, AND J. G. SEELYE. 1985. Survival of lake trout eggs and fry reared in water from the upper Great Lakes. J. Great Lakes Res. 11: 520-529.

MAC, M. J., T. R. SCHWARTZ, AND C. C. EDSALL. n.d. Correlating PCB effects on fish reproduction using dioxin equivalents. U.S. Fish Wildl. Serv., Ms Rep. 1 p.

MacCALLUM, W. A. 1981. A review of the eastern Lake Superior lake trout quotas. Ont. Min. Nat. Resour., Lake Superior Fish. Assess. Unit Ms Rep., Thunder Bay.

MacCRIMMON, H. R., AND E. SKOBE. 1970. The fisheries of Lake Simcoe. Ont. Dep. Lands Forests, Toronto. 140 p.

MacCRIMMON, H. R., C. D. WREN, AND B. L. GOTS. 1983. Mercury uptake by lake trout, *Salvelinus namaycush*, relative to age, growth, and diet in Tadenac Lake with comparative data from other Precambrian Shield lakes. Can. J. Fish. Aquat. Sci. 40: 114-120.

MACHNIAK, K. 1975. The effects of hydroelectric development on the biology of northern fishes (reproduction and population dynamics. IV. Lake trout, *Salvelinus namaycush* (Walbaum). Environ. Can., Fish. Mar. Serv. Tech. Rep. 530. 52 p.

MacLEAN, J. A., D. O. EVANS, N. V. MARTIN, AND R. L. DesJARDINE. 1981. Survival, growth, spawning distribution, and movements of introduced and native lake trout (*Salvelinus namaycush*) in two inland Ontario lakes. Can. J. Fish. Aquat. Sci. 38: 1685-1700.

MacLEAN, N., J. GUNN, F. HICKS, P. IHSSEN, M. MALHIOT, AND T. MOSINDY. 1990. Genetic and environmental factors affecting the physiology and and ecology of lake trout. Lake trout synthesis. Ont. Min. Nat. Resour., Toronto. (In prep.)

MAGNUSON, J. J. 1976. Managing with exotics - A game of chance. Trans. Am. Fish. Soc. 105: 1-9.

MAITLAND, P. S. 1972. Loch Lomond: man's effects on the salmonid community. J. Fish. Res. Board Can. 29: 849-860.

MALINS, D. C., B. B. McCAIN, D. W. BROWN, S.-L. CHAN, M. S. MYERS, J. T. LANDALL, P. G. PROHASKA, A. J. FRIEDMAN, L. D. RHODES, D. G. BURROWS, W. D. GRONLUND, AND H. O. HODGINS. 1984. Chemical pollutants in sediments and diseases of bottom-dwelling fish in Puget Sound, Washington. Environ. Sci. Technol. 18: 705-713.

MANNY, B. A., AND T. A. EDSALL. 1989. Assessment of lake trout spawning habitat quality in central Lake Huron by submarine. J. Great Lakes Res. 15: 164-173.

MARCUS, M., W. HUBERT, AND S. ANDERSON. 1984. Habitat suitability index models: lake trout (exclusive of the Great Lakes). U.S. Fish Wildl. Serv. Rep. FWS/OBS-82/10.84: 12 p.

MARSHALL, T. R., R. A. RYDER, C. J. EDWARDS, AND G. R. SPANGLER. 1987. Using the lake trout as an indicator of ecosystem health - application of the dichotomous key. Great Lakes Fish. Comm. Tech. Rep. No. 49. 35 p.

MARTENS, D. W., AND J. A. SERVIZI. 1974. Acute toxicity of municipal sewage to fingerling sockeye salmon. Int. Pacific Salmon Fish. Comm. Prog. Rep. 29. 18 p.

MARTIN, N. V. 1952. A study of the lake trout, *Salvelinus namaycush* in two Algonquin Park, Ontario, lakes. Trans. Am. Fish. Soc. 81: 111-137.

MARTIN, N. V. 1954. Catch and winter food of lake trout in certain Algonquin Park lakes. J. Fish. Res. Board Can. 11: 5-10.

MARTIN, N. V. 1955. The effect of drawdowns on lake trout reproduction and the use of artificial spawning beds. Trans. 20th North Am. Wildl. Conf.: 263-271.

MARTIN, N. V. 1956. Reproduction of lake trout in Algonquin Park, Ontario. Trans. Am. Fish. Soc. 86: 231-244.

MARTIN, N. V. 1970. Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opeongo, Ontario. J. Fish. Res. Board Can. 27: 125-146.

MARTIN, N. V., AND L. J. CHAPMAN. 1965. Distribution of certain crustaceans and fishes in the region of Algonquin Park, Ontario. J. Fish. Res. Board Can. 22: 969-976.

MARTIN, N. V., AND F. E. J. FRY. 1973. Lake Opeongo: the ecology of the fish community and of man's effects on it. Great Lakes Fish. Comm. Tech. Rep. 24. 34 p.

MARTIN, N. V., AND C. H. OLVER. 1976. The distribution and characteristics of Ontario lake trout lakes. Ont. Min. Nat. Resour., Fish Wildl. Res. Br., Res. Rep. 97. 30 p.

MARTIN, N. V., AND C. H. OLVER. 1980. The lake charr, *Salvelinus namaycush*, p. 205-277. *In* E.K. Balon [ed.] Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk bv Publ., The Hague, The Netherlands. 928 p.

MATHERS, J. S. 1978. The effects of highway construction on Galt Creek, Ont. Min. Nat. Resour., Min. Trans. Commun. Rep. No. 1. 115 p.

MATHERS, R. A., AND P. A. JOHANSEN. 1985. The effects of feeding ecology on mercury accumulation in walleye (*Stizostedion vitreum*) and pike (*Esox lucius*) in Lake Simcoe. Can. J. Zool. 63: 2006-2012.

MATTICE, C. R. 1977. Forest road erosion in northern Ontario: a preliminary analysis. Can. Forest Serv. Dept. Fish. Environ. Rep. No. 0-X-254. 27 p.

MATUSZEK, J. E., B. J. SHUTER, AND J. M. CASSELMAN. 1990. Age specific shifts in lake trout growth and abundance: long-term changes following a cisco introduction. Trans. Am. Fish. Soc. (In press)

McCAIG, R. S., AND J. W. MULLAN. 1960. Growth of eight species of fishes in Quabbin Reservoir, Massachusetts, in relation to age of reservoir and introduction of smelt. Trans. Am. Fish. Soc. 89: 27-31.

McCASHION, J. D., AND R. M. RICE. 1983. Erosion of logging roads in northwestern California: how much is avoidable? J. Forest. Jan. 1983: 23-26.

McCRIMMON, H. R. 1958. Observations on the spawning of lake trout, *Salvelinus namaycush*, and the post-spawning movement of adult trout in Lake Simcoe. Can. Fish Cult. 23: 1-9.

McFADDEN, J. T. 1977. An argument supporting the reality of compensation in fish populations and a plea to let them exercise it, p. 153-182. *In* W. VanWinkle [ed.] Assessing the effects of power-plant induced mortality on fish populations. Pergamon Press, New York. 380 p.

McKIM, J. M., AND D. A. BENOIT. 1971. Effects of long-term exposures of copper on survival, growth and reproduction of brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 28: 655-662.

McKIM, J. M., G. F. OLSON, G. W. HOLCOMBE, AND E. P. HUNT. 1976. Long-term effect of methylmercuric chloride on three generations of brook trout: toxicity, accumulation, distribution and elimination. J. Fish. Res. Board Can. 33: 2726-2739.

McMURTRY, M. J. 1986. Susceptibility of lake trout (*Salvelinus namaycush*) spawning sites in Ontario to acidic meltwater. Ont. Min. Nat. Resour., Ont. Fish. Acidification Rep. Ser. No. 86-01. 14 p.

McMURTRY, M. J., AND B. J. SHUTER. 1985. The Lake Opeongo creel survey. Ont. Fish. Tech. Rep. Ser. No. 19. 16 p.

McMURTRY, M. J., D. L. WALES, W. A. SCHEIDER, G. L. BEGGS, AND P. E. DIMOND. 1989. Relationship of mercury concentration in lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieui*) to the physical and chemical characteristics of Ontario lakes. Can. J. Fish. Aquat. Sci. 46: 426-434.

McNAMEE, P. J., M. L. JONES, L. A. GRIEG, C. H. WEDELES, D. R. MARMOREK, AND L. P. RATTIE. 1987. Effects monitoring for resource protection guidelines in Ontario. ESSA Rep. to Ont. Min. Nat. Resour. 226 p.

MEMORANDUM OF INTENT. 1983. Memorandum of intent on transboundary air pollution. Impact assessment working group, Washington, DC and Ottawa, Ont.

MERRIMAN, D. 1939. Squam lake trout. Boston Soc. Nat. Hist. Bull. 75: 3-10.

MILLS, K. H., S. M. CHALANCHUK, L. C. MOHR, AND I. J. DAVIES. 1987. Responses of fish populations in lake 223 to eight years of experimental acidification. Can. J. Fish. Aquat. Sci. 44: 114-125.

MUNKITTRICK. K. R., AND D. G. DIXON. 1988. Growth, fecundity and energy stores of white sucker (*Catostomus commersoni*) from lakes containing elevated levels of copper and zinc. Can. J. Fish. Aquat. Sci. 45: 1355-1365.

MUNKITTRICK, K. R., AND D. G. DIXON. 1989. Use of white sucker (*Catostomus commersoni*) populations to assess the health of aquatic ecosystems exposed to low-level contaminant stress. Can. J. Fish. Aquat. Sci. 46: 1455-1462.

NICHOLSON, J. A., N. W. FOSTER, AND I. K. MORRISON. 1982. Forest harvesting effects on water quality and nutrient status in the boreal forest. *In* Proc. Can. Hydrology Symp. 1982. NRCC Publ. No. 20548.

NIIMI, A. J., AND C. Y. CHO. 1983. Laboratory and field analysis of pentachlorophenol (PCP) accumulation by salmonids. Water Res. 17: 1791-1795.

NORTHCOTE, T. G. 1972. Kootenay Lake: man's effects on the salmonid community. J. Fish. Res. Board Can. 29: 861-865.

NUMANN, W. 1972. The Bodensee: effects of exploitation and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 833-847.

ODUM, E. P., J. T. FINN, AND E. H. FRANZ. 1979. Perturbation theory and the subsidy-stress gradient. BioScience 29: 349-352.

OLVER, C. H. 1980. Lake trout lakes geographical reference atlas. Ont. Min. Nat. Resour., Fish. Br. Ms. Rep., Toronto. (Computer printout)

OLVER, C. H. 1988. The regulation of harvest in lake trout sport fisheries: a review and appraisal. Ont. Min. Nat. Resour. Ms Rep., Toronto. 67 p.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1982. Partitioning yields estimated from the morphoedaphic index into individual species yields. Report of SPOF Working Group Number Twelve. 71 p.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1983. Strategic planning for Ontario fisheries. Policy development. The identification of overexploitation. Report of SPOF Working Group Number Fifteen. 83 p.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1985. Proposed evaluation of the Rondeau Bay artificial reef project. Ont. Min. Nat. Resour. unpubl. Ms. 49 p.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1988a. 1985 review of the life history of the Pacific salmon and their interaction with other salmonids. Report from the Pacific Salmon Working Group, May 1988. 33 p.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1988b. Atlas of smallmouth bass lakes in Ontario. Ont. Min. Nat. Resour., Fish. Br., Toronto. 47 p.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1988c. Atlas of walleye lakes in Ontario. Ont. Min. Nat. Resour., Fish. Br., Toronto. 105 p.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1988d. Atlas of muskellunge lakes in Ontario. Ont. Min. Nat. Resour., Fish. Br., Toronto.

ONTARIO MINISTRY OF NATURAL RESOURCES, AND DEPARTMENT OF FISHERIES AND OCEANS. 1988. Sportfishing in Ontario, 1985. Dep. Fish. Oceans, Sci. Info. Publ. Br., Ottawa. 12 p.

ONTARIO MINISTRY OF THE ENVIRONMENT. 1981. Outlines of analytical methods. Laboratory Services Branch, Toronto. 246 p.

ONTARIO MINISTRY OF THE ENVIRONMENT. 1989. The zebra mussel, *Dreissena polymorpha*: A synthesis of European experiences and a preview for North America. Ont. Min. Environ., Water Resour. Br., Toronto. 76 p. + Appendices.

ONTARIO MINISTRY OF THE ENVIRONMENT, AND ONTARIO MINISTRY OF NATURAL RESOURCES. 1988. Guide to eating Ontario sport fish. Ont. Min. Environ., Commun. Serv. Br., Toronto. 303 p.

ORGAN, W. L., G. L. TOWNES, M. O. WALTER, R. B. PELLETIER, AND D. A. REIGE. 1978. Past and presently known spawning grounds of fishes in Michigan coastal waters of the Great Lakes. Draft. Mich. Dep. Nat. Resour., Fish. Div. Tech. Rep. #78-7.

PARKS, J. W., J. A. SUTTON, AND J. D. HOLLINGER. 1984. Mercury contamination of the Wabigoon/English/ Winnipeg River system, causes, effects and possible remedial measures. Min. Supply Serv. Can.

PATERSON, R. J. 1968. The lake trout (*Salvelinus namaycush*) of Swan Lake, Alberta. Alberta Dep. Lands Forests, Fish Wildl. Div. Res. Rep. 2. 149 p.

PAULY, D. 1980. On the relationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39: 175-192.

PAYNE, N. R., R. M. KORVER, D. MacLENNAN, S. J. NEPSZY, B. J. SHUTER, T. J. STEWART, AND E. R. THOMAS. 1990. The harvest potential and dynamics of lake trout stocks in Ontario. Lake trout synthesis. Ont. Min. Nat. Resour., Fish. Br., Toronto. 72 p.

PECK, J. W. 1982. Extended residence of young-of-the-year lake trout in shallow water. Trans. Am. Fish. Soc. 111: 775-778.

PETERMAN, R. M., W. C. CLARK, AND C. S. HOLLING. 1979. The dynamics of resilience: shifting stability domains in fish and insect systems, p. 321-341. *In* R.M. Anderson, B.D. Turner, and L.R. Taylor [ed.] Population dynamics. Blackwell Scientific Publ., Oxford.

PICKERING, A. D. 1981. The concept of biological stress, p. 1-9. *In* A.D. Pickering [ed.] Stress and fish. Academic Press, London. 367 p.

PIMM, S. L. 1984. The complexity and stability of ecosystems. Nature (Lond.) 307: 321-326.

PIMM, S. L., H. L. JONES, AND J. DIAMOND. 1988. On the risk of extinction. Am. Nat. 132: 757-777.

PLAMONDON, A. P., A. GONZALEZ, AND Y. THOMASSIN. 1982. Effects of logging on water quality: comparison between two Quebec sites. Can. Hydrology Symp. 1982. NRCC Publ. No 20548.

PLUARG. 1978. Environmental management strategy for the Great Lakes system. Int. Ref. Group on Great Lakes Pollution from Land Use Activities. Int. Joint Comm., Windsor, Ont.

POWER, G. 1978. Fish population structure in Arctic lakes. J. Fish. Res. Board Can. 35: 53-59.

POWER, G., AND J. GREGOIRE. 1978. Predation by freshwater seals on the fish community of Lower Seal Lake, Quebec. J. Fish. Res. Board Can. 35: 844-850.

PREVOST, G. 1957. Use of artificial and natural spawning beds by lake trout. Trans. Am. Fish. Soc. 86: 258-260.

PRICE, K. S., D. A. FLEMER, J. A. TAFT, G. B. MACKIERNAN, W. NEHLSEN, R. B. BIGGS, N. H. BURGER, AND D. A. BLAYLOCK. 1985. Nutrient enrichment of Chesapeake Bay and its impact on the habitat of striped bass: a speculative hypothesis. Trans. Am. Fish. Soc. 114: 97-106.

PRIEDE, I. G. 1977. Natural selection for energetic efficiency and the relationship between activity level and mortality. Nature 267: 610-611.

PRIEDE, I. G. 1985. Metabolic scope in fishes, p. 33-64. *In* P. Tytler and P. Calow [ed.] Fish enegetics: new perspectives. John Hopkins, University Press, MD.

PURYCH, N. A. 1975. The 1968, 1969 and 1971 winter lake trout sport fishery of Summers Lake. Ont. Min. Nat. Resour., Blind River Dist. Ms Rep. 22 p.

PYCHA, R. L., AND G. R. KING. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey and stocking, 1950-70. Great Lakes Fish. Comm. Tech. Rep. 28. 34 p.

RAPPORT, D. J., H. A. REGIER, AND T. C. HUTCHINSON. 1985. Ecosystem behavior under stress. Am. Nat. 125: 617-640.

RAPPORT, D. J., H. A. REGIER, AND C. THORPE. 1981. Diagnosis, prognosis, and treatment of ecosystems under stress, p. 269-280. *In* G.W. Barrett and R. Rosenberg [ed.] Stress effects on natural ecosystems. Chap. 19. John Wiley and Sons, New York. 305 p.

RAWSON, D. S. 1961. The lake trout of Lac la Ronge, Saskatchewan. J. Fish. Res. Board Can. 18: 423-462.

REED, S. W., A. DEMAYO, AND M. C. TAYLOR. 1979. Guidelines for surface water quality. Vol. 1. Inorganic chemical substances - mercury. Inland Waters Directorate, Water Quality Br., Ottawa, Ont.

REGIER, H. A., AND K. H. LOFTUS. 1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 959-968.

REISER, D. W., AND T. C. BJORNN. 1979. Habitat requirements of anadromous salmonids. I. Influence of forest and rangeland management on anadromous fish habitat in the western United States and Canada. USDA Forest Serv., General Tech. Rep. PNW-96. Pacific Northw. Forest and Range Exp. Sta., Portland, OR. 54 p.

RICHMOND, L. A., C. D. WREN, AND P. M. STOKES. 1988. Facts and fallacies concerning mercury uptake by fish in acid-stressed lakes. Water Air Soil Pollut. 37: 465-473.

RICKER, W. E. 1959. The origin of two glacial relict crustaceans in North America, as related to Pleistocene glaciation. Can. J. Zool. 37: 871-893.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191. 382 p.

RIEBESELL, J. J. 1974. Paradox of enrichment in competitive systems. Ecology 55: 183-187.

RITCHIE, J. C. 1972. Sediment, fish, and fish habitat. J. Soil Water Conserv. 27: 124.

ROMBOUGH, P. J. 1988. Respiratory gas exchange, aerobic metabolism and effects of hypoxia during early life, p. 59-144. *In* W.S. Hoar and D.J. Randall [ed.] Fish physiology, Volume XIA. Academic Press, New York. 546 p.

ROSENZWEIG, M. L. 1971. Paradox of enrichment: destabilization of exploited ecosystems in ecological time. Science 107: 385-387.

ROTTIERS, D. V., AND R. A. BERGSTEDT. 1981. Swimming performance of young lake trout after chronic exposure to PCB's and DDE. U.S. Fish Wildl. Serv. Fish. Bull. 105: 23-28.

ROYCE, W. F. 1951. Breeding habitats of lake trout in New York. U.S. Fish Wildl. Serv. Fish. Bull. 52: 59-76.

RYDER, R. A. 1957. Winter fishing pressure on lake trout, Port Arthur District, 1957. Ont. Dep. Lands Forests, Port Arthur Dist. Ms Rep. 4 p.

RYDER, R. A., AND C. J. EDWARDS [eds.]. 1985. A conceptual approach for the application of biological indicators of ecosystem quality in the Great Lakes Basin. Rep. to the Great Lakes Sci. Advis. Board, Int. Joint Comm., Windsor, Ont. 169 p.

RYDER, R. A., AND L. JOHNSON. 1972. The future of salmonid communities in North American oligotrophic lakes. J. Fish. Res. Board Can. 29: 941-949.

RYDER, R. A., AND S. R. KERR. 1984. Reducing the risk of fish introductions - a rational approach to the management of integrated cold-water communities, p. 510-533. *In* Proc. European Inland Fish Advisory Comm. (EIFAC) Symp. EIFAC Tech. Pap. 42. FAO, Rome.

SAKAMOTO, M. 1966. The chlorophyll amount in the euphotic zone in some Japanese lakes and its significance in the photosynthetic production of phytoplankton community. Bot. Mag. Tokyo 79: 77-88.

SAMIS, W. G. A. 1970. A winter and summer creel census on Ranger Lake, 1968. Ont. Dept. Lands Forests, Sault Ste. Marie Dist. Ms Rep. 17 p.

SAMSEL, G. L., Jr. 1973. Effects of sedimentation of the algal flora of a small recreational impoundment. Water Resour. Bull. 9: 1145-1152.

SCHINDLER, D. W. 1975. Whole-lake eutrophication experiments with phosphorus, nitrogen and carbon. Verh. Int. Verin. Limnol. 19: 3221-3231.

SCHINDLER, D. W., E. J. FEE, AND T. RUSZCZYNSKI. 1978. Phosphorus inputs and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and in similar lakes. J. Fish. Res. Board Can. 35: 190-196.

SCHINDLER, D. W., R. W. NEWBURY, K. G. BEATY, J. PROKOPOWICH, T. RUSZCZYNSKI, AND J. A. DALTON. 1980. Effects of a windstorm and forest fire on chemical losses from forested watersheds and on the quality of receiving streams. Can. J. Fish. Aquat. Sci. 37: 328-334.

SCHRECK, C. D. 1981. Stress and compensation in teleostean fishes: response to social and physical factors, p. 295-321. *In* A.D. Pickering [ed.] Stress and fish. Academic Press, London. 367 p.

SCHUMACHER, R. E. 1961. Some effects of increased angling pressure on lake trout populations in four northeastern Minnesota lakes. Minn. Dep. Conserv., Div. Game Fish., Fish Ser. 3: 20-42.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 182. 966 p.

SELYE, H. 1973. The evolution of the stress concept. Am. Sci. 61: 692-699.

SELYE, H. 1976. The stress of life. McGraw-Hill, New York. 515 p.

SHUTER, B. J., J. E. MATUSZEK, AND H. A. REGIER. 1987. Optimal use of creel survey data in assessing population behaviour: Lake Opeongo lake trout (*Salvelinus namaycush*) and smallmouth bass (*Micropterus dolomieui*) 1936-83. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 229-238.

SHUTER, B. J., D. A. SCHLESINGER, AND P. A. ZIMMERMAN. 1983. Empirical predictors of annual surface water temperature cycles in North American lakes. Can. J. Fish. Aquat. Sci. 40: 1838-1845.

SIGLER, J. W., T. C. BJORNN, AND F. H. EVEREST. 1984. Effects of chronic turbidity on density and growth of steelheads and coho salmon. Trans. Am. Fish. Soc. 113: 142-150.

SLY, P. G. 1986. Lake trout spawning habitat studies in Lake Ontario, Georgian Bay - Lake Huron, Lake Superior, and parts of the Finger Lakes (N.Y.). Environ. Canada, Nat'l. Water Res. Inst. Can. Centre for Inland Waters, Burlington, Ont. (Unpubl. Ms)

SLY, P. G. 1988. Interstitial water quality of lake trout spawning habitat. J. Great Lakes Res. 14: 301-315.

SLY, P. G., AND C. P. SCHNEIDER. 1984. The significance of seasonal changes on a modern cobble-gravel used by spawning lake trout, Lake Ontario. J. Great Lakes Res. 10: 78-84.

SLY, P. G., AND C. C. WIDMER. 1984. Lake trout (*Salvelinus namaycush*) spawning habitat in Seneca Lake, New York. J. Great Lakes Res. 10: 168-189.

SMITH, B. R., AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in lakes Huron, Michigan, and Superior: history of invasion and control, 1936-78. Can. J. Fish. Aquat. Sci. 37: 1780-1801.

SMITH, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667-693.

SMITH, S. H. 1970. Species interactions of the alewife in the Great Lakes. Trans. Am. Fish. Soc. 4: 754-765.

SMITH, S. H. 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 717-730.

SONZOGNI, W. C., T. J. MONTEITH, E. SEIBEL, AND J. M. ARMSTRONG. 1977. Great Lake shoreline erosion: chemical loading. Int. Assoc. Great Lakes Res., 20th Conf. Great Lakes Res., Univ. Mich., Ann Arbor, MI.

SPANGLER, G. R., N. R. PAYNE, J. E. THORPE, J. M. BYRNE, H. A. REGIER, AND W. J. CHRISTIE. 1977. Responses of percids to exploitation. J. Fish. Res. Board Can. 34: 1983-1988.

STAUFFER, T. M. 1979. Effects of DDT and PCB's on survival of lake trout eggs and fry in a hatchery and in Lake Michigan, 1973-1976. Trans. Am. Fish. Soc. 108: 178-186.

STAUFFER, T. M. 1981. Collecting gear for lake trout eggs and fry. Prog. Fish-Cult. 43: 186-192.

STAUFFER, T. M., AND W. C. WAGNER. 1979. Fish predation on lake trout eggs and fry in the Great Lakes, 1973-1978. Mich. Dep. Nat. Resour., Fish. Res. Rep. No. 1864. 13 p.

STEEDMAN, R. J., AND H. A. REGIER. 1987. Ecosystem science for the Great Lakes: perspectives on degradative and rehabilitative transformations. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 95-103.

STEWART, D. J., J. F. KITCHELL, AND L. B. CROWDER. 1981. Forage fish and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110: 751-763.

SUNS, K., G. HITCHIN, B. LOESCHER, E. PASTOREK, AND R. PEARCE. 1987. Metal accumulations in fishes from Muskoka-Haliburton lakes in Ontario (1978-1984). Ont. Min. Environ., Rexdale, Ont. 38 p.

TANG, A. J. S., A. AHMED, AND M. A. LUSIS. 1986a. Summary: some results from the APIOS atmospheric deposition monitoring program (1981-1984). Ont. Min. Environ., Air Resour. Br. ARB-110-86, Toronto. 33 p.

TANG, A. J. S., W. H. CHAN, D. H. S. CHUNG, AND M. A. LUSIS. 1986b. Precipitation and air concentrations and wet and dry deposition fields of pollution in Ontario - 1983. Ont. Min. Environ., Air Resour. Br., Toronto. 99 p.

TARAZONA, J. V., M. J. MUNOZ, J. A. ORTIZ, M. O. NUNEZ, AND J. A. CAMARGO. 1987. Fish mortality due to acute ammonia exposure. Aquacult. Fish. Manage. 18: 167-172.

THOMPSON, R., R. CHESSELL, AND K. ROCHE. 1984. Summary of commercial fishery quota development in Lake Nipigon, 1984. Ont. Min. Nat. Resour., Nipigon Dist. Ms Rep. 8+ p.

THURSTON, R. V., R. C. RUSSO, AND C. E. SMITH. 1978. Acute toxicity of ammonia and nitrite to cutthroat trout fry. Trans. Am. Fish. Soc. 107: 361-368.

THURSTON, R. V., R. C. RUSSO, AND G. A. VINOGRADER. 1981. Ammonia toxicity to fishes. Effect of pH on the toxicity of the un-ionized ammonia species. Environ. Sci. Tech. 15: 837-840.

THURSTON, R. V., R. C. RUSSO, C. M. FETTEROLF, JR., T. A. EDSALL, AND Y. M. BARBER, JR. 1979. A review of the EPA Red Book: Quality criteria for water. Water Quality Sect., Am. Fish. Soc., Bethesda, MD. 313 p.

VERDUIN, J. 1964. Changes in western Lake Erie during the period 1948-62. Verh. Int. Verh. Limnol. 15: 639-644.

VOLLENWEIDER, R. A. 1968. The scientific basis of lake and stream eutrophication, with particular reference to phosphorus and nitrogen as eutrophication factors. Tech. Pap. O.E.C.D. Parcs. DAS/CSI/68 27: 1-82.

WAGNER, W. C. 1981. Reproduction of planted lake trout in Lake Michigan. N. Am. J. Fish. Manage. 1: 159-164.

WARNER, K., AND O. C. FENDERSON. 1963. The salmon and trout fishery of Fish River lakes, Maine. Trans. Am. Fish. Soc. 92: 193-201.

WEBB, R. W., AND J. R. BRETT. 1973. Effects of sublethal concentrations of sodium pentachlorophenate on growth rate, food conversion efficiency, and swimming performance in underyearling sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 30: 499-507.

WEDEMEYER, G. A., AND D. J. McLEAY. 1981. Methods determining the tolerance of fishes to environmental stressors, p. 247-275. *In* A.D. Pickering [ed.] Stress and fish. Academic Press, London. 367 p.

WEITHMAN, A. S., AND M. A. HAAS. 1984. Effects of dissolved-oxygen depletion on the rainbow trout fishery in Lake Taneycomo, Missouri. Trans. Am. Fish. Soc. 113: 109-124.

von WESTERNHAGEN, H. 1988. Sublethal effects of pollutants on fish eggs and larvae, p. 253-346. *In* W.S. Hoar and D.J. Randall [ed.] Fish physiology, Vol. XIA. Academic Press, New York. 546 p.

WILBER, C. G. 1983. Turbidity in the aquatic environment. An environmental factor in fresh and oceanic waters. Charles C. Thomas, Springfield, MA. 133 p.

WILTON, M. L. 1985. Water drawdown and its effects on lake trout (*Salvelinus namaycush*) reproduction in three south-central Ontario lakes. Ont. Fish. Tech. Rep. Ser. No. 20. 9 p.

WOBESER, G. 1975. Acute toxicity of methyl mercury chloride and merauric chloride for rainbow trout (*Salmo gairdneri*) fry and fingerlings. J. Fish. Res. Board Can. 32: 2005-2013.

WOOD, C. M., AND D. G. McDONALD. 1982. Physiological mechanisms of acid toxicity to fish, p. 197-226. *In* T.A. Haines and R.E. Johnson [ed.] Acid rain/fisheries. Proc. Int. symp. acid precipitation and fishery impacts in northeastern North America. Cornell Univ., Ithaca, NY, Aug. 2-5, 1981. Northeast Div. Am. Fish. Soc., Bethesda, MD. 357 p.

WREN, C. D., AND H. R. MacCRIMMON. 1983. Mercury levels in the sunfish, *Lepomis gibbosus*, relative to pH and other environmental variables of Precambrian Shield lakes. Can. J. Fish. Aquat. Sci. 40: 1737-1744.

YAREMCHUCK, G. C. B. 1986. Results of a nine year study (1972-80) of the sport fishing exploitation of lake trout (*Salvelinus namaycush*) on Great Slave and Great Bear lakes, NWT: the nature of the resource and management options. Can. Tech. Rep. Fish. Aquat. Sci. 1436: 80 p.

YOUNGS, W. D., AND R. T. OGLESBY. 1972. Cayuga Lake: effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 787-794.

ZARET, T. M., AND R. T. PAINE. 1973. Species introductions in a tropical lake. Science (Washington, D.C.) 182: 449-455.

MAPS
NOT
FILMED

CARTES
OMISES